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EDITORIAL NOTE

Among the wetlands of Brazil, the Pantanal occupies a very important position. With its almost 200,000 km^2, this tropical wetland harbours a diverse flora and fauna which is a result of the intensive interactions of flooding in rivers, lakes, natural channels, creeks and streams. Knowledge of the Pantanal biodiversity is of prime importance for its conservation and the identification of the ecosystem services of this large wetland.

This volume constitutes an effort to characterise the Pantanal´s biodiversity and it is one more contribution from the *Brazilian Journal of Biology* to improve knowledge on Neotropical biodiversity.

The Editorial Board

PRESENTATION

The United Nations has declared 2010 the "International Year of Biodiversity", to celebrate biological diversity and emphasise its importance in our lives. Brazil is one of the signatories of the Convention on Biological Diversity and is implementing its recommendations towards conservation and sustainable use of its territory. Additionally, the United Nations General Assembly declared 2011 as the International Year of Forests to raise awareness on sustainable management, conservation and sustainable development of all types of forests.

The *Pro-reitoria de Pesquisa e Pós-graduação* (responsible for graduate studies and research) of the Anhanguera/Uniderp university is proud to give its shared support, along with the *Instituto Internacional de Ecologia* (International Institute of Ecology -IIE), in producing this special number of the *Revista Brasileira de Biologia (Brazilian Journal of Biology)* on the Biodiversity of the Pantanal. It aims to provide unified scientific information, secure regional academic contributions and improve the conservation of our important neighbouring biome. Authors include researchers from different institutions of our region as well as from national agencies. The volume is organised to emphasise scientific and cultural knowledge on biodiversity, focussing on its conservation under natural circumstances.

The focus on biodiversity reflects the increasing interest and concern among Brazilian academics and the general public for the importance of the diversity of life within the Pantanal. This increased motivation and attention are expressed in the Brazilian Constitution of 1988, declaring the biome a National Heritage Area, as well as the international recognition with the declaration of Wetland of International Importance under the Convention on Wetlands (RAMSAR), and as a Biosphere Reserve, granted by the United Nations Educational, Scientific and Cultural Organization (UNESCO).

This volume brings together a number of articles expressing different views on a diverse array of subjects as a collaborative action for the same purpose: emphasising the value of academic research for increased knowledge about the richness of species and natural habitat conservation. The main message of this special volume is to stress the benefits of knowing and conserving the Pantanal's biota, which our society cannot afford to lose. Scientists, the media, and the public in general are aware of the many convincing arguments for the importance of our biodiversity. Individual attitudes are important, but institutional action, which motivates the publication of this volume, contributes to our placing a higher value on biology, from molecules to ecosystems, and to avoiding the tragedies associated with species loss.

The 200th anniversary of Charles Darwin's birth, celebrated on 12 February of 2009, was a gratifying event, given his position as the father of modern biology; his theory of evolution and the broader principle of natural selection are strikingly present in the Pantanal's biodiversity. His celebrated *Origin of Species* serves as a stimulus, reminding us how powerfully a publication brings insights and practical benefits together towards a more hopeful future for protected nature.

Prof. Dr. Guilherme Marback Neto
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Biodiversity of the Pantanal: its magnitude, human occupation, environmental threats and challenges for conservation

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The Pantanal biome is a wetland – a floodplain in a geographic depression – formed by the Paraguay River and its tributaries from the left bank: Bento Gomes, Cuiabá, São Lourenço-Itiquira, Taquari, Negro, Aquidauana-Miranda, Nabileque, and Apa. The Paraguay River and its tributaries form the Upper Paraguay Basin and drain into the Pantanal depression, running southward between highlands to the west and the upland plateaus to the east, where the tributaries have their springs. These large rivers are shaped largely by type of soil, water flow rate, levels of dissolved oxygen, nutrient loads, temperature, and type of river bed. The rivers are slow moving when they leave the upland plateaus surrounding the floodplain and meet the flatlands, where they periodically overflow their banks.

The maze of fluctuating water levels within this sedimentary floodplain, plus annual nutrient cycling though biogeochemical cycles with influx of nutrients, particulate material, microorganisms and invertebrates form a dynamic ecosystem, with a complex mosaic of habitats and diverse and abundant wildlife. The four phases of the hydrological cycle (water rising or flooding, flood season, receding water or drainage season, and dry season) are essential for wildlife. The annual tides of the rivers, causing seasonal flooding, result in availability of feeding and reproductive niches for wildlife.

Macroinvertebrates. The diversity of benthonic macroinvertebrates (zoobenthos such as decapods, molluscs, oligochaetes, insect larvae which feed upon microoganisms and algae) were estimated in 70 taxa (Takeda et al., 2000). Zoobenthos are important in the food chain because they serve as food for fish, birds, mammals and other animal groups. Ostracoda (aquatic crustacea) and Nematoda (free living non-parasitic roundworms) are the two most abundant groups.

Crustacean diversity. Shrimps and crabs are represented by 10 species and the shrimp *Macrobrachium amazonicum* and the crabs *Dilocarcinus pagei, Sylviocarcinus australis, Trichodactylus borellianus* and *Valdivia camerani* are found in field surveys (Magalhães, 2000). These decapod crustaceans play an important role in ecological processes of the Pantanal's aquatic ecosystem since they participate in the trophic chain as herbivores, predators, decomposers and are prey for fish and other animal groups.

Plant diversity. Three articles discussing plants of the Pantanal are presented in this volume.

Fish. Fish are an important resource, both ecologically and socially. Britiski et al. (1999) listed 263 species for the Pantanal. However, a survey carried out in the Negro River region of the Pantanal showed that 19% of the species collected are believed to be new to science (Willink et al., 2000). This list does not include species living in the upper river habitats. The number of fish species increases from the headwaters (plateau upland region or *planalto)* to the base of the drainage (Pantanal).

Because of the great variety of feeding and reproductive niches for fish, the Pantanal harbours high species abundance. Fishing is of fundamental social-economic importance for local people. In addition, fishing for sport is one of the incentives to bring tourists to the region. Junk et al. (2006) discuss more on fish diversity of the Pantanal.

Fish resources in the Pantanal have been recognised according to their use as:

- a fundamental biotic component of the ecosystem, supporting the local biodiversity and being part of it;
- food for subsistence and income of local people;
- of interest for sport fishing;
- a genetic resource;
- an ornamental resource.

Herpetofauna. Compared to other Brazilian biomes, the Pantanal presents a herpetofauna low in diversity but high in abundance. There are 135 herpetofaunal species living on the plains (40 species of anuran amphibians, three species of turtles, 25 species of lizards, two species of amphisbaenians, 63 species of snakes and two of crocodilians (Junk et al., 2006). A survey carried out in the southern Pantanal recorded 41 anuran and 24 reptile species (Strüssman et al., 2000).

During the rainy season the region presents vigorous populations of amphibians, thanks to the expansion of favourable habitats. Three reproductive activity patterns are recognised among the species: continuous, explosive, and prolonged; 50% of the species were explosive breeders (Prado, 2003).

Many Pantanal species are distributed throughout Brazil, such as the rococo-toad *Bufo paracnemis* and the Chaco-frog *Leptodactylus chaquensis,* the dwarf-tree frogs *Hyla fuscovaria*; *Hyla acuminata, Hyla raniceps,* the green-leaf-frog *Scinax acuminatus,* the marbled-tree-frog *Phrynohyas venulosa* and the common-washroom-frog

Scinax cf. *nasicus*. The abundant tine green frog *Lysapus limellus* has a semi-aquatic habit, lives on floating plants, eating insects and other invertebrates (Alho et al., 2002).

About half of the anuran species in the Pantanal live in trees. Some species, such as the spotted-tree-frog *Hyla punctata,* are associated with permanent bodies of water (rivers and ponds) and others, such as the purple-barred-tree-frog *Hyla raniceps*, the green-leaf-frog *Scinax acuminatus*, the yellow-and-black-tree-frog *Scinax fuscovarius,* tolerate droughts but the population suddenly grows when flooding comes, usually October to May. Frogs are also more vocal during this period.

The tiny clicking-frog *Lysapsus limellus* lives on floating vegetation and also vocalises by day. Also vocalising on floating plants are the paradox-frog *Pseudis paradoxa* and the speckled-bellied-frog *Physalaemus albonotatus.* During the rainy season this *Physalaemus albonotatus* frog is one of the most conspicuous and vocal when they join in sonorous choir, even by day.

Amphibians with terrestrial habits are the leaf-toad *Bufo typhonius*, the frogs *Chiasmocleis mehelyi*, *Leptodactylus elenae, Physalaemus cuvieri,* and the arboreal frog *Phrynohyas venulosa*. Another tiny frog living in dead tree holes in the forest is *Chiasmocleis mehelyi, which* has only recently been reported in the Pantanal. Some other species live at the water line between aquatic and terrestrial habitats, such as *Pseudopaludicola* aff. *falcipes*, *Leptodactylus fuscus*, *Leptodactylus podicipinus*, *Bufo paracnemis*, *Bufo granulosus* and *Elachistocleis* cf. *ovale*. A colourful aposematic species is *Phyllomedusa hypochondrialis.*

Among reptiles, there are more than 30 species of snake. The yellow-anaconda *Eunectes notaeus* is very common on the plains and is small in size compared to the other species, the green anaconda *E. murinus* that lives at the edge of the Pantanal and may reach 5 m in size, some observations reporting a size of 6-8 m. Another large snake is the water-queen *Hydrodynastes gigas,* which occurs at the borders of gallery forests or patches of savannas looking for toads, their preferred food. Small nocturnal snakes, which prey upon frogs, are *Thamnodynastes* cf. *strigilis*, *Leptodeira annulata* and *Liophis poecilogyrus.*

There are four species of poisonous snakes in the Pantanal: the Brazilian-lancehead *Bothrops moojeni*, the Neuwid'lancehead *B. neuwiedi*, the neotropical-rattlesnake C*rotalus durissus* and the Pantanal-coral-snake *Micrurus tricolor*.

The occurrence of species within the sub-regions of the Pantanal varies according to the local species composition and distribution, depending on the influence of the nearby biomes such as the Chaco, the Cerrado and the Amazonia. Among the snakes of the northern sub-region of Poconé, for example, Strüssmann and Sazima (1993) observed that the most abundant species are *Eunectes notaeus, Helicops leopardinu* and *Hydrodynastes cf strigilis.* While the southern sub-region of Nhecolândia presented different species composition with *Leptodeira annulata, Liophis typhlus* and *Lystrophis mattogrossensis,* snakes common throughout the Brazilian Cerrado. The same pattern is observed for amphibians, but with difference in local abundance, which is more remarkable in the Pantanal for these species.

There is one terrestrial turtle, the red-footed-tortoise *Geochelone carbonaria* plus one aquatic species, the large-headed-Pantanal-swamp-turtle *Acanthochelys macrocephala.* The caiman *Caiman crocodillus* is abundant and conspicuous, particularly during the dry season, being one of the symbols of the Pantanal.

Twenty species of lizards are known for the region, all preferring dry habitats except for the Pantanal-caiman-lizard *Dracaena paraguayensis* which lives in the water. Two lizard species, *Kentropyx viridistriga* and *Mabuya guaporicola,* are able to swim and dive to escape predators. Common geckos, *Phyllopezus policaris* and *Polychrus acutirostris,* exploit the branches of bushes. Three lizards can be easily observed searching for prey on the ground or rapidly escaping from intruders: *Tupinambis merianae*, *Ameiva ameiva* and *Cnemidophorus ocellifer.* The green-iguana *Iguana iguana* is also seen in trees along the rivers or on riverbanks.

Bird Diversity. There are 444 bird species recorded only for the floodplains, 665 species when the uplands are included and 837 species for the Cerrado biome (Tubelis and Tomas, 2002; Silva, 1995).

A bird field guide published in Portuguese "Aves do Brasil: Pantanal & Cerrado" and in English, "Birds of Brazil: Pantanal & Cerrado" (Gwynne et al., 2010) pointed out 740 species for both biomes highlighting the birdlife to inspire bird watching to enjoy the biomes' vibrant ecosystems and natural heritage, addressing an ecological context an conservation messages.

More discussion on bird diversity is provided by Junk et al (2006). Bird species with aquatic habits are very common and abundant, including egrets such as species of the genera *Casmerodius, Egretta, Ardea, Tigrisoma, Botaurus,* in addition to the wood-stork *Mycteria americana,* the maguari-stork *Ciconia maguari* and the jabiru *Jabiru mycteria.* Kingfishers are present with 5 species of the two genera *Ceryle* and *Choroceryle.* Other aquatic species are the southern-screamer *Chauna torquata*, the muscovy-duck *Cairina moschata,* the fulvous-whistling-duck *Dendrocygna bicolor,* the white-faced-whistling-duck *D. viduata,* the black-bellied-whistling-duck *D. autumnalis* and the Brazilian-duck *Amazonetta brasilienses.* Among birds of prey are the snail-kite *Rosthramus sociabilis,* the black-collared-hawk *Busarellus nigricollis*, the great-black-hawk *Butteogallus urubitinga* and the Crane-hawk *Geranospiza caerulescens.* Parrots are abundant. I observed a group of 206 turquoise-fronted-parrots *Amazona aestiva* in the SESC Reserve at Barão de Melgaço. There are 19 species of psitasids including the hyacinth macaw *Anodorhynchus hyacinthinus.*

Conservation. The biome's biodiversity has been impacted by unsustainable socio-economic practices, including:

- deforestation (conversion of natural vegetation into pastures for cattle, conversion of Cerrado vegetation into crop fields in the uplands where the headwaters are located, charcoal production, habitat loss and alteration); data on deforestation of the Pantanal biome for the period 1976-2008 show about 15% of natural vegetation loss with degradation reaching near 60% in the surrounding uplands (Silva et al., 2010);

- environmental contaminants (petroleum-based inputs of agricultural chemicals, mainly in the uplands, mercury contamination in gold mining, in addition to iron ore, manganese, and calcium carbonate, sewage and domestic waste from the great majority of the cities surrounding the Pantanal);
- infrastructure and unplanned human occupation (large cargo convoys navigate the large rivers of the Pantanal, mainly the Paraguay and Cuiabá rivers, and vessels damage riverbanks with oil spills and waste; road kills of wildlife along roads throughout the wetlands);
- unregulated tourism (predatory invasion of waterfowl nesting grounds, sport fishing with illegal campsites in gallery forests spreading waste);
- fragility of law enforcement (some protected areas, hunting activities, commercial and sport fishing, deforestation with soil degradation are generally out of the control of the environmental agencies, with consequent impacts on habitats and biodiversity loss);
- introduction of exotic species (there are a considerable number of introduced species within the natural habitats, both deliberate and accidental: tucunaré fish, feral pig, *Limnoperma fortunei* mussel and others).

The major economic activities in terms of land occupation are cattle ranching and tourism. Many large ranches have been subdivided into small farms, modifying the original arrangement of extensive cattle ranching. In recent years, over-fishing has been seen to be a major problem in the region.

Some major projects and studies have been carried out:

- The EDIBAP (Study for the Integrated Development of the Upper Paraguay River Basin), between 1977 and 1989;
- The PCBAP (Plan for Conservation of the Upper Paraguay Basin), conducted in 1997;
- The ANA/GEF/UNEP/OAS (Strategic Action Program for the Integrated Management of the Pantanal and the Upper Paraguay River Basin), carried out by ANA (Brazilian National Water Agency) in 2005;
- INAU – Instituto Nacional de Ciência e Tecnologia em Áreas Úmidas (The National Institute of Science and Technology in Wetlands). This new institute aims to carry out research to support public policies for the conservation and sustainable management of natural resources in the Pantanal. The working structure of INAU facilitates the integration of the Pantanal Research Center (CPP) and the Universidade Federal de Mato Grosso (Federal University of Mato Grosso) in Cuiabá;
- NGO's ACTION PLANS – Different NGOs play important role on biodiversity conservation of the Pantanal. For example, the diagnosis entitled "*Monitoring Alterations in Vegetation and Land Use in the Brazilian Portion of the Upper Paraguay River Basin*" was carried out by the nongovernmental organizations: Ecoa - Ecologia e Ação, Conservation International, Avina Foundation, SOS Pantanal and WWF - Brasil and received technical support from Embrapa Pantanal. The purpose of the study was to make a detailed analysis of changes in vegetation patterns and land use that took place in the period from 2002 to 2008. The diagnostic study shows that compared to other Brazilian biomes like the Atlantic Forest formations, the Pantanal is relatively well-conserved although it is very vulnerable especially to impacts occurring in the highland regions of the Upper Paraguay River basin. While the lower floodplain region has 86.6% of its natural vegetation cover intact, only 43.5% of the highland plateau areas have their original vegetation;
- ACADEMIC CONTRIBUTIONS – Regional Universities such as the UFMT (Universidade Federal do Mato Grosso = Federal University of Mato Grosso); the UFMS (Universidade Federal do Mato Grosso do Sul = Federal University of Mato Grosso do Sul), the state Universities for both states, and private universities like the Anhanguera-Uniderp (Universidade para o Desenvolvimento do Estado e da Região do Pantanal = University for the Development of the State and the Region of the Pantanal) are contributing with academic research including thesis and dissertations;
- CPAP (Embrapa Pantanal = Embrapa Pantanal Research Center) of Embrapa (Empresa Brasileira de Pesquisa Agropecuária = Brazilian Agricultural Research Corporation) – The Center was implanted in Corumbá in 1975. Its mission is to make technological solutions viable for the sustainable development of the Pantanal agribusiness with the valorization of nature, including fauna and flora conservation;
- There have been different programmes and activities to establish initiatives to identify critical priorities for the conservation of biodiversity, including the creation of new protected areas. The conservation strategy should consider the Pantanal as a whole biome, connecting all sub-regions and different ecosystems, with protected areas representative of the major sub-region, as

well as considering the role of ecological corridors for the dispersion of species and integration of the adjacent biomes.

The challenge for conservation of the magnificent biodiversity of the Pantanal increases as time passes and, unfortunately, we can testify to the loss of habitats and species, not as a result of natural selection, but because of human disturbance. If on the one hand scientific knowledge is fundamental for the implementation of conservation, on the other hand, scientific results alone cannot solve the problems of environmental disruption. However, we are convinced that the scientific information available in this special number of the *Brazilian Journal of Biology* will play a vital role in conserving the regional biodiversity of the Pantanal biome. It will add important scientific knowledge to environmental awareness, providing a basis for government action and encouraging us all to practise humanitarian values to protect our natural treasures through ethical attitudes.

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Geomorphology and habitat diversity in the Pantanal

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(With 4 figures)

Abstract

The present study deals with the inter-relations in the relief which forms the Bacia do Alto Rio Paraguay (BAP) in mid-west Brazil. The overall aim is to discuss the relationship between relief forms and the biodiversity of the Pantanal. The BAP is a natural environmental system with contrasts in two of the compartments on which it is formed: the plateau, the most elevated compartment, highly transformed by human activities, and the plain which forms the Pantanal, which is more preserved and less transformed in relation to productive activities. The analysis was performed based on publications with a geomorphologic focus, examining the different relief units of the BAP and the dynamics of the revealing processes of landscape change which the Pantanal has undergone since the end of the Pleistocene.

Keywords: Pantanal geomorphology, biodiversity, relief.

Geomorfologia e a biodiversidade no Pantanal

Resumo

O presente estudo tem como objetivo abordar a inter-relação entre os compartimentos do relevo brasileiro que compõem a Bacia do Alto Paraguai - BAP, para discutir as formas de relevo e a biodiversidade do Pantanal. A abordagem fundamenta-se na compreensão das diferentes formas do terreno, associando ao fato que a BAP é um sistema ambiental natural que tem contrastes nos dois compartimentos que a compõem: o planalto, o compartimento mais elevado, fortemente transformado por atividades humanas; e a planície, que constitui o Pantanal mato-grossense, mais conservada e pouco transformada, quanto ao uso com atividades produtivas. A análise foi realizada a partir de publicações com enfoques geomorfológicos, abordando as diferentes unidades do relevo da BAP e o entendimento da dinâmica dos processos reveladores de que o Pantanal passa desde o fim do Pleistoceno, com processos de mudanças da paisagem.

Palavras-chave: geomorfologia do Pantanal, biodiversidade, relevo.

1. Introduction

Biodiversity itself is a relatively recent term, and it has only recently been studied in relation to other areas of scientific knowledge, such as geomorphology. There have been few studies on the biodiversity of the Pantanal Mato-Grossense which deal with the relief forms at the interface of the abiotic, biotic and anthropic components of its complex environmental system (Franco and Pinheiro, 1982; Silva, 1984; Ross, 1990; Ab'Saber, 1996; Alho and Gonçalves, 2005).

The spatial arrangement of the relief forms is considered an important variable for understanding the diversity of the landscapes and one of the indicators of the dynamic balance in the protection of biodiversity.

Since relief is the result of endogenous and exogenous forces, including climatic and tectonic factors, it helps to explain the distribution, diversity, extinction and performance of living beings on the earth's surface (Silva, 1984).

The definition of geomorphologic units is based on the supposition that the planet is the result of the interaction between living beings and the physical-geographical environment. This is illustrated in the works of Tricart (1972), in the form of a matrix. While the morphogenetic processes modify the surface of the Earth they generate instability and harm the multiple and fragile balances towards which the systems incline, connected by a chain of interdependences, such as that shown in Figure 1.

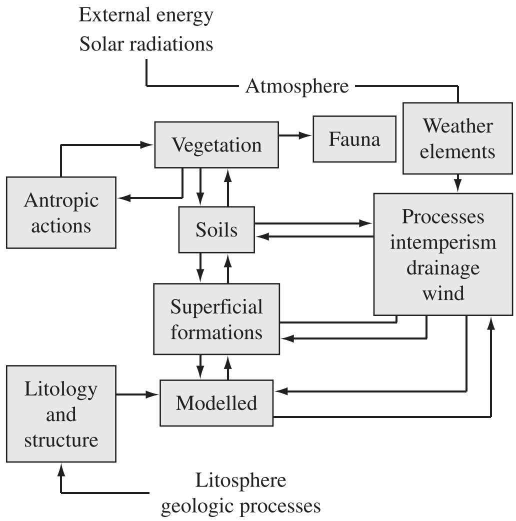

Figure 1. Flow chart elaborated based on Tricart´s conception (1972).

In the Tricartian matrix the models are situated at the interface of abiotic, biotic and anthropic components. Tricart considered that an eco-dynamic unit is characterised by a certain dynamic of the environment and has repercussions on biosinesis.

Studies by Ross (2006) have been based on a combination of information about natural vegetation, lithology, relief forms, soils, climate and biogeography. These have culminated in the mapping of the territorial macrospaces in Brazil, which also show the different types of land use by society.

The Ross classification (2006) was built on this integrated view. Ross's analysis of the BAP places the plateau in the category of savannah that has been highly transformed by economic activities. In contrast, the plain where the Pantanal Mato-Grossense lies is placed in the slightly transformed group of natural environmental systems, such as the fluvial plains of Araguaia and Guaporé and some marine plains.

The Pantanal Mato-Grossense is a natural system presenting a great diversity in flora and fauna. Even though it is occupied by human activities, the Pantanal presents low transformation intensity in the natural vegetation cover caused by productive activities such as farming and mining. However, it has undergone very strong impacts from other activities. The two main threats are the uncontrolled use of soil in the areas surrounding the Pantanal plain, which are drier and flood free; and the consequences of deforestation on the plateau. The latter is a result of many development plans for Central Brazil, none of which considered the natural connection between the high and low parts of the region (Conservação International, 2009).

The plateau is also intensively used for agriculture and cattle breeding. Human occupation is less invasive in the natural vegetation cover of the plains. On the plateau region the natural cover represents 42% of the total territory and on the plain the percentage is 87% (Conservação International, 2009; Abdon et al., 2007).

Alho (2008, p. 958) provides an analysis of the key factors that have impacted the Pantanal's ecosystems:

> The present landscape arrangement and natural ecosystems are the result of three factors: 1) geological changes occurring since the Quaternary, which probably influenced the drainage patterns of the region; 2) the pronounced differences in annual cycles of wet and dry seasons plus exceptional periods of long flooding or droughts causing retraction or expansion of the Pantanal, thus, a phenomena related to greater or lesser primary productivity and ecological succession and 3) areas related to human intervention such as pastures, artificial ponds or introduced trees near the ranch houses.

Assine (2003) and Mercante et al. (2007). indicate the existence of complex processes of change in the landscape of the Pantanal, resulting from the sedimentary dynamic in alluvial fans. In these fan regions the landscape changes continuously because of sedimentation and by avulsion processes. These cause changes in the river beds, such as those occurring in the Taquari River.

The Pantanal is a highly changeable quaternary sedimentary plain. Its understanding is vital to projects for use and occupation, as well as conservation and preservation, and needs to be based on interdisciplinary knowledge (Ab'Saber, 1988; Alho and Gonçalves, 2005; Assine et al., 2008; Mercante and Paiva, 2009; Mercante and Santos, 2009). This study is placed within this context, in order to identify aspects of relief forms which are important to the biodiversity of the Pantanal Mato-Grossense. First we examine the relationship between plateau and plain by classifying the compartments and cartography of the relief units. Next, we describe different relief forms in the Pantanal, with special attention to the formation of fluvial fans. Last, some conceptual lessons will be highlighted in order to detail the innumerous landscape features that characterise the region's relief and shelter its rich biodiversity.

2. Study Area

The Pantanal, located between parallels 15º and 20º S and meridians 55º and 59º W, is a vast low flat plain. It features a depositional tract of sandy sediments derived from the plateaus of sedimentary basins, forming huge alluvial fans and lacustrine and fluvial environments. Accumulation areas are geomorphologically highlighted on the plain with seasonal floods and other areas of fluvio-lacustrine accumulation.

The Pantanal Mato-Grossense has worldwide value and is recognised as the world's largest continuous inland wetland. It ranges in altitude from 100 to 150 m, presents flat relief, and lies within a significant geological unit known as the Bacia do Alto Paraguay (BAP) (Figure 2).

3. Procedures

We analyse texts and cartographic examples, integrating methodological focus based on the idea that relief forms are

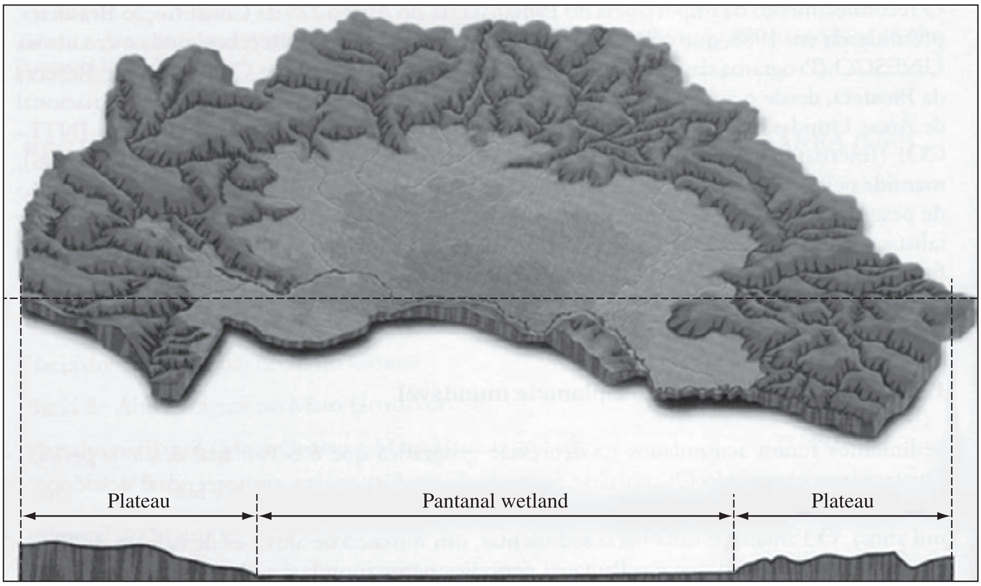

Figure 2. Illustration of the diagram block showing aerial view from West and the flat texture representing the unit of the Pantanal flats and the Pantanal itself and the remaining wrinkled texture representing the surrounding plateau. The inferior part of the illustration shows the topographic profile elaborated from north to south axis starting with the high parts of the plateau followed by the depressed part of the flat and finishing on the plateaus of the extreme south. Adapted from Alho and Gonçalves (2005).

direct and permanent products of the interactions between internal and external energy flows. The methodology used in this study is based on a literature review of publications presenting mappings of the different geomorphologic compartments of the BAP, where we can find the plain and the marshlands of the Paraguay River, known as the Pantanal Mato-Grossense.

The concepts of Ross (2006) have been adopted for the generation of the BAP map, highlighting the relief macroforms of the surrounding plateau and including the Pantanal Mato-Grossense plain. Ross (2006) provides the basis to understand that the Pantanal Mato-Grossense is an active sedimentary basin being filled by a considerable layer of sediments that come from the surrounding plateau. He demonstrates that the plain and the marshland are natural environmental systems which have undergone little transformation, taking into account information on the characteristics of natural vegetation, geology, geomorphology, pedology, climate and biogeography.

In order to understand the sedimentary processes the studies by Tricart (1972, 1982) were used. These are based on the premise that geomorphologic evolution generates differentiation in the relief units. On the Pantanal Plain, in particular, the sedimentary dynamics involves the formation of alluvial fans.

4. Discussion

Relief, as one of the components of the natural environment, presents a great diversity of shapes. These shapes are important for all living beings, which need a physical support, or biotopic.

The relief of the Bacia do Alto Paraguai is marked by the contrast between the plain which is the Pantanal, with areas ranging from 50 to 150 m above sea level, and the elevated lands of the plateau (200 to 1,200 m above sea level).

4.1. Classification and relief units

According to the classification of the geomorphologic units of Brazil elaborated by Ross (2006) the plain and the Pantanal of the River Paraguay are surrounded to the east, northeast, south and southeast by macroforms of Brazilian relief (Figure 3).

In the cartographic synthesis with the different geomorphologic units of the macroforms of Brazilian relief, the plain and the Pantanal of the Paraguay River, as mapped and denominated by Ross (2006), are one large unit considered a slightly transformed environment despite being occupied by human activities.

The data and information presented in Table 1 reveal one of the important aspects of the Bacia do Alto Paraguay, which are the relief macroforms which surround the plain and the Pantanal of the Paraguay River. These geomorphologic units are important in order to understand the existing complexity in the processes of accumulation and the fluvial processes on the plain.

4.2. The plain and the Pantanal of the Paraguay River

The plain represented in Figure 3 as a large white area presents low intensity of transformation of the

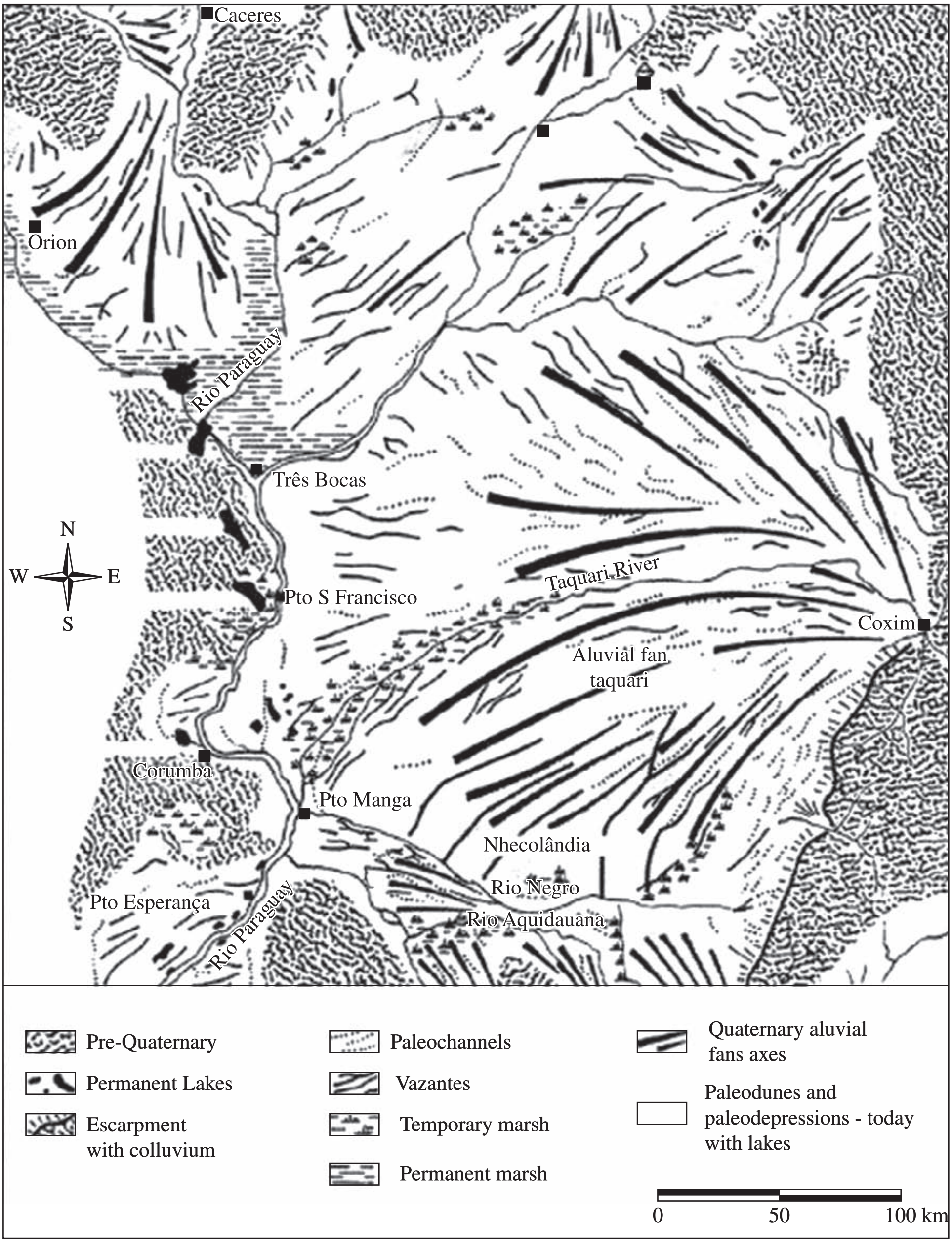

Figure 3. It is shown in the cartographic product about the geomorphology of Pantanal, elaborated by Tricart, the design of the alluvial fans, and the observations about the geomorphologic partitioning.

natural vegetation cover by interventions of productive activities, such as extensive cattle breeding, subsistence agriculture, fishing, mining and timber extraction. In these less transformed environments the natural conditions are highly diversified, and mosaic plant cover is formed. There are various types of words, also highlighted on the map: on the wetlands, the fluvial dykes and the uplands known as "cordilheiras". All these environments are extremely rich in fauna and flora and have been used for many different human activities.

Based on the interpretation of orbital images available in the 1980s, Tricart (1982) mapped the main areas of past action of eolic processes and used cartography to present the alluvial fans of the Pantanal, whose distributary pattern of the rivers were highlighted by the fluvial paleochannels.

The author also analysed geomorphological conditions in the areas with lagoons. He considered that these regions, nowadays occupied by innumerous circular and semi-circular lagoons like those present in the Nhecolândia Pantanal, are a relic of non-active alluvial fans.

Table 1. Geomorphologic units in the surrounding of Pantanal Mato-Grossense, based on Ross classification (2006). Adapted from Ross (2006).

Relief forms	Altitude(m)	Litology	Soils
Paraná basin plateau and lowlands			
Ample hills with convex summits – mid-north. Chapadas – flat surfaces on the North-Northeast Patamares and structural scarps associated to hills and mound-hills with convex summits. Scarps on the edges	400 - 700 700 - 800 500 - 1,400	Sandstones Sandstones associated with clayish detritical covering Basalts, diabases and rhyolite.	Red-yellow-sandy latosoils Sandy-red claysoils Clayish red latosoils Nitosoil cambic soils, litolic
Alto Paraguai Plateau and residual elevations			
Elongated elevations on anticlinal crystals – synclinal – mountainous relief Valleys and closed anticlinal depressions Ample synclinal valleys Intermountain depressions	600 - 800 300 - 400 200 - 300	Calcareous silicified sandstone Shales arkose	Litolic neosoil Cambic neosoil Rocky outcrops Red claysoils
Bodoquena Plateau			
Surfaces of hills with convex summits, fragments with flat summits	600 - 900	Migmatite, gneisses, amphybolite, quartzite, carbonatic rocks and granites	Red claysoils Litolic neosoil
Cuiabana Depression			
Vast mound-hills with slightly carved valleys Small asymmetrical crests	150 - 400	Metasandstones – phyllite – quartzite	Red-yellow plintosoils and claysoils
Alto Paraguai-Guaporé Depression			
Vast mound-hills with flat summits, slightly carved valleys Fluvial plains	150 - 250	Shales Arkose - inconsolidated sandy sendiments	Quartzarenic neosoils Yellow Latosoils
Miranda Depression			
Vast mound-hills with flat summits Not too deep valleys	150 - 200	Metasandstones, phyllite, quartzitos, limestone	Red-yellow claysoils

On Tricart's (1982) map, it is important to highlight the outline of several alluvial fans, of which the largest is known as the Taquari Mega-fan (Figure 4).

The plains and the Paraguay River Pantanal cover a vast surface with extremely flat topography and altitudes ranging from 80 m near the Paraguay River to 150 m in higher areas. They present a complex hydrographic network of rivers originating from the surrounding scarps, running through narrow alluvial plains subject to seasonal floods with permanent flooded areas. All rivers originating in the east, northeast, south and southeast coalesce on the left riverbank of Alto Paraguay.

Due to different flooding patterns these areas have been denominated according to flood accumulation areas and plains. These areas are traditionally known as "Pantanais Mato-Grossenses" or Pantanal sub-regions.

Those units are denominated "pantanais" (swamps) due to frequent flooding by superficial waters. However, this name is inappropriate as the region does not present swamps as a whole. The plains are identified according to different genetic formation processes, such as fluvial plains (linked to the Paraguay River and its affluents) and fluvio-lacustrine plains (in interfluvial positions among the rivers of the basin).

The flood areas are directly related to the topographic variations and to the kind of soil which characterises the behaviour of superficial and sub superficial waters. From this, low, average and high flood areas are known, positioned in different ways in relation to the main axis of local drainage. The altitude varies between 150 and 180 m further from the drainage axis, but areas near drainage lie at below 100 m altitude. This is also the case at the confluences of

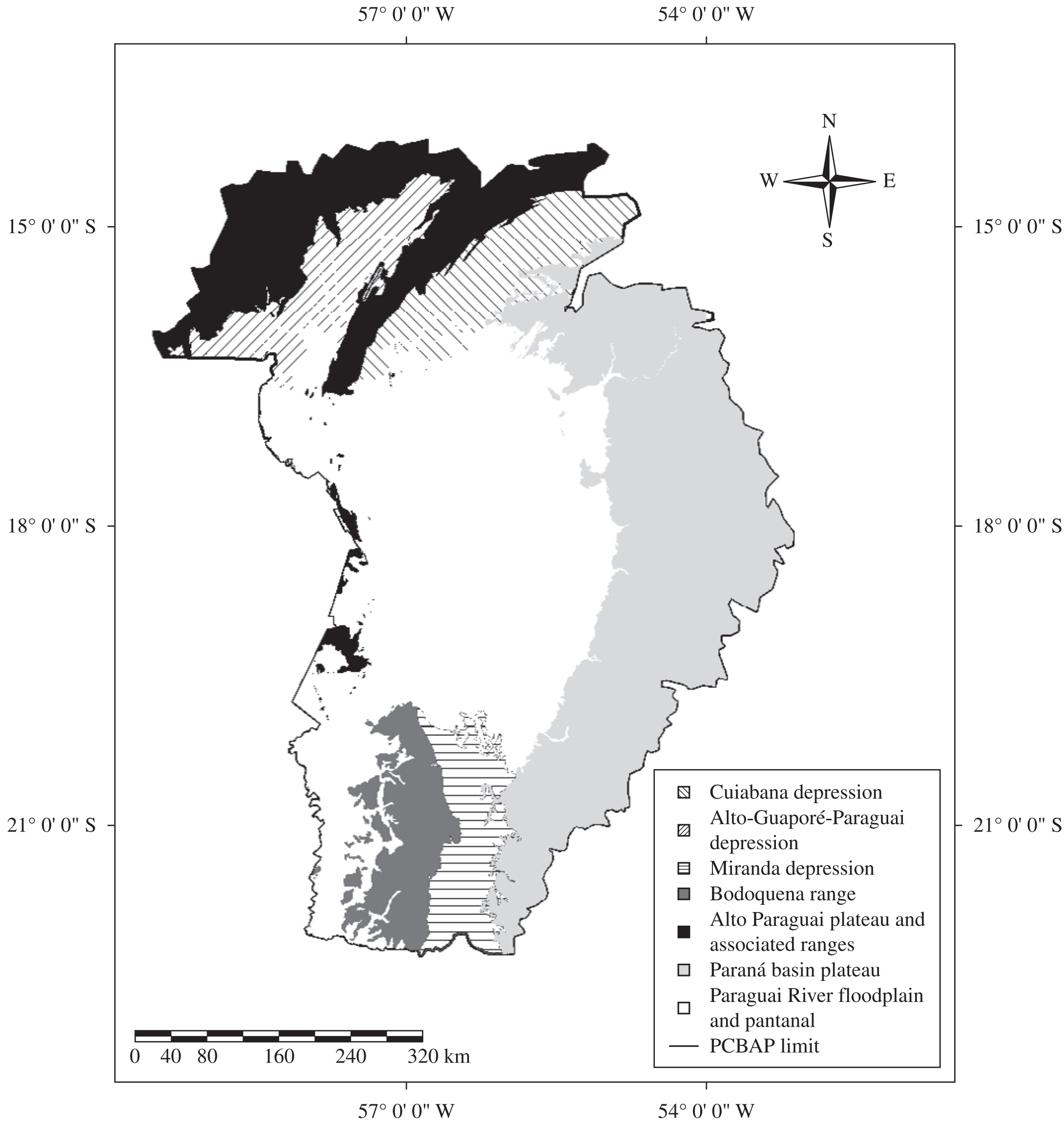

Figure 4. BAP map presenting the macroforms of the relief of the surrounding plateau and the plain of the Pantanal Mato-Grossense.

the main fluvial courses, with variable flooding periods ranging from three to four months in weak flooding areas up to nine months in strong flooding areas; there are also areas which remain flooded all year long.

The flooded areas are modelled on recent sediment deposits along the valleys characterised by the presence of marginal dams, sandy bars, islands and circular and semi-circular shaped lagoons. Some features in these areas are identified by the following regional names:

a) baias: small depressions in the terrain presenting different forms (circular, semicircular or irregular), which may contain water. They may or may not be covered by aquatic species of plants;
b) cordilleras: ridges of firm terrain, locally denominated "cordilheiras". The term "cordilheira" is used for the innumerable marginal paleodykes or clay ridges, which are usually unflooded, ranging from one to three metres above the field levels and which cover strips of the terrain (on average longer than they are wide). These are preferred areas for the location of cattle ranches, and are very much used as a refuge for "swamp" livestock and by the regional fauna during the flood season;
c) vazantes: vast elongated depressions located between the "cordilheiras" which serve as fluvial courses up to many kilometres long and which

may be intermittent or perennial, or may connect bays or streams;

d) corixos: channels with temporary or perennial drainage which connect adjacent baias or even bigger water courses. They are more powerfully erosive than the "vazantes" (presenting more excavated beds which are usually narrower and deeper);
e) capões or caapões: islands of trees usually in an area located from 0.3 to 30 m above the field. It is slightly hilly, measuring from five to one hundred metres in diameter, where the vegetation becomes denser and the trees are from many different species of flora in the savannah;
f) *oxbow lakes*: these lakes are on the banks of many rivers and have a significant role in the freshwater biodiversity as they are reproduction and feeding sites for many species. They may present high connectivity with the original system (the river) due to the relief, distance and the magnitude of the flood rhythm. They are often known as baias;
g) fluvial avulsion: fluvial avulsion starts with the breaking of marginal dykes and sedimentation on adjacent low areas which become flooded during flooding seasons. The breaks in marginal dykes are known by the communities in the Pantanal as "arrombados". During the floods part of the water starts to flow towards the flood plain through the "arrombado" and the channel may split, originating a distributary channel. In case the new distributary channel becomes the main channel, which usually implies abandonment of the old channel, leading to a drastic change in the river course; and
h) fluvial plains: These are the various strips of land where sediments accumulate. This is a result of the surface drainage difficulties along practically all the watercourses of the Paraguay River and its main tributaries which flow down the plateau towards the plain, such as the rivers Bento Gomes, Cuiabá, São Lourenço, Itiquira, Taquari, Negro, Aquidauana, Miranda, Nabileque and Apa.

Many factors must be considered when analysing how exogenous processes act on the fluvial plains, in the superficial drainage of water (speed, discharge and kinds of flow), subterranean infiltration and drainage, time of residence of the water in the system, water table fluctuation, kinds of transport of the sediments (channelled or spread flow), deposit of sediments on the riverbed, sedimentary processes on the flood plains, avulsion and divergence of the channels.

The processes of deposition and erosion are constant. This is highlighted by the migration and abandonment of the beds, by the formation of marginal dykes, changes in channels by avulsion processes and the breaks known as arrombados. These processes of alterations in the landscape are intense in the alluvial fan of the River Taquari (Mercante et. al., 2007).

The fluvio-lacustrine plains correspond to the deposits of the marginal areas in the lagoons in the hydrodynamic processes of flooding and "vazantes" where they vary in the quality of the carried sediments.

It is important to mention the hills scattered along isolated areas of the plain, which are usually round and from 150 to 200 m high on average. During the flooding season they stand out in the flooded areas like islands covered in vegetation. The hills located on the west side are not part of the plain, but are eroded areas of the Amolar Mountains.

5. Final Considerations

Despite offering generic data and being more classificatory for BAP units, the analysis of published articles makes it possible, by means of the conceptions adopted by their authors, to relate geomorphologic dynamics and relief forms with the biodiversity of the plain and the Pantanal of the Paraguay River, i.e., the Pantanal Mato-Grossense.

The approach made it possible to reach some conclusions:

1) The landscape of the Pantanal has become a symbol for biodiversity and environmental challenge with a double mission: to enrich the biodiversity and not allow the degradation of Pantanal with predatory and inadequate uses;
2) The Pantanal is definitely a complex and heterogeneous space cell inland in the South American continent and in order to establish biodiversity conservation and recovery strategies the link with its geomorphology is indispensable;
3) The Pantanal Mato-Grossense is a natural system which has been slightly transformed by human action and at the same time a fragile microcosm of rich biodiversity against the threat of turning into an environmental system that is highly degraded and modified by human actions;
4) Its geomorphologic evolution process, which has been going on for thousands of years with a sedimentary dynamic on the alluvial fans, is continuously changing due to the alterations in accumulation and deposit of sediments as well as due to the dynamics of its drainage system; and
5) Such a complex relationship on a wet area forms a picture of an exceptional landscape in Brazil with the recognition of its importance on the international scene.

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Hydrological cycle

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(With 5 figures)

Abstract

The Pantanal hydrological cycle holds an important meaning in the Alto Paraguay Basin, comprising two areas with considerably diverse conditions regarding natural and water resources: the Plateau and the Plains. From the perspective of the ecosystem function, the hydrological flow in the relationship between plateau and plains is important for the creation of reproductive and feeding niches for the regional biodiversity. In general, river declivity in the plateau is 0.6 m/km while declivity on the plains varies from 0.1 to 0.3 m/km. The environment in the plains is characteristically seasonal and is home to an exuberant and abundant diversity of species, including some animals threatened with extinction. When the flat surface meets the plains there is a diminished water flow on the riverbeds and, during the rainy season the rivers overflow their banks, flooding the lowlands. Average annual precipitation in the Basin is 1,396 mm, ranging from 800 mm to 1,600 mm, and the heaviest rainfall occurs in the plateau region. The low drainage capacity of the rivers and lakes that shape the Pantanal, coupled with the climate in the region, produce very high evaporation: approximately 60% of all the waters coming from the plateau are lost through evaporation. The Alto Paraguay Basin, including the Pantanal, while boasting an abundant availability of water resources, also has some spots with water scarcity in some sub-basins, at different times of the year. Climate conditions alone are not enough to explain the differences observed in the Paraguay River regime and some of its tributaries. The complexity of the hydrologic regime of the Paraguay River is due to the low declivity of the lands that comprise the Mato Grosso plains and plateau (50 to 30 cm/km from east to west and 3 to 1.5 cm/km from north to south) as well as the area's dimension, which remains periodically flooded with a large volume of water.

Keywords: Pantanal of Brazil, water resources, hydrologic regime.

Ciclo hidrológico

Resumo

O ciclo hidrológico do Pantanal guarda um significado importante na bacia do Alto Paraguai, a qual compreende duas áreas em condições consideravelmente diversas no que se refere aos recursos hídricos e naturais, o planalto e a planície. Sob o enfoque de função ecossistêmica, o fluxo hidrológico na relação planalto-planície é importante para a criação de nichos reprodutivos e alimentares para a biodiversidade regional. Em geral, a declividade dos rios no planalto é de 0,6 m/km enquanto que a declividade na planície é de 0,1 a 0,3 m/km, e o ambiente na planície é caracteristicamente sazonal e mantém uma diversidade de espécies exuberantes em abundância, inclusive de animais ameaçados de extinção. Ao encontrar a planície, a superfície plana faz diminuir o fluxo de água no leito dos rios e, na época de chuva, os rios transbordam seus leitos, inundando a planície. A precipitação média anual da bacia é de 1.396 mm, variando entre 800 mm e 1.600 mm, e as maiores chuvas são observadas na região do planalto. A baixa capacidade de drenagem dos rios e lagos que formam o Pantanal e o clima da região fazem com que, aproximadamente, 60% de todas as águas provenientes do planalto sejam perdidas por evaporação. A bacia do Alto Paraguai, incluindo o Pantanal, embora tenha abundante disponibilidade de recursos hídricos, apresenta situações de escassez em determinadas sub-bacias e em determinadas épocas do ano. As condições climáticas por si só não são suficientes para explicar as diferenças que são observadas no regime do rio Paraguai e de alguns de seus afluentes. A complexidade do regime hidrológico do rio Paraguai está relacionada à baixa declividade dos terrenos que integram as planícies e pantanais mato-grossenses (de 50 a 30 cm/km no sentido leste-oeste e de 3 a 1,5 cm/km de norte para o sul) e também à extensão da área que permanece periodicamente inundada com grande volume de água.

Palavras-chave: Pantanal do Brasil, recursos hídricos, regime hidrológico.

The opinions expressed in the text are the sole responsibility of the authors.

1. Introduction

The *Alto* Paraguay Basin, covering roughly 600,000 sq km, has 362,376 km in Brazil, comprising 4.3% of the national territory, that basin holds considerable importance in the strategic context of water resources management for Brazil, Bolivia and Paraguay, which share it not only for its dimensions, but for being home to the Pantanal, one of the largest stretches of flooded areas in the planet, with 147,574 sq km, constituting a link between the Cerrados in Brazil, and the *Chaco* in Bolivia and Paraguay.

The drastically seasonal environment of the Pantanal boasts a diversity of exuberant and abundant species, including endangered species. Aspects of flooding and drainage, topography and nutrients strongly influence the landscapes and the supplies of feeding and reproductive niches for the native fauna.

The present study, which adopts an ecosystem function focus, aims to demonstrate that the hydrologic flow of the Pantanal is related to the geographic position of the Upper Paraguay Basin, with its plateau and plain compartments that interact to form reproductive and feeding niches for the biodiversity of the region.

2. Procedures Adopted

Data were extracted from integrated management action programmes for the Pantanal and Upper Paraguay Basin (ANA, 2008), in which the combined strategies aim to demonstrate that the Pantanal is important for the management of water resources in Brazil and the neighbouring countries that share this basin – Bolivia and Paraguay.

In order to correlate water resources with the rich biodiversity of the Pantanal, data were inserted containing ecosystem approaches (Alho and Gonçalves, 2005).

3. Pantanal and the Ecosystem Context

The Pantanal is a lowland area subject to periodical flooding, which is nationally and internationally recognised for the exuberance of its biodiversity, as a humid area of utmost importance in the globe. It is part of the Upper Paraguay River Basin (BAP) and is formed by the Paraguay River and, in Brazil, by its tributaries, especially the ones located on the left bank.

The river Paraguay is one of the major tributaries of the Prata River Basin, the second largest river basin in South America, outsized only by the Amazon Basin, expanding through a total area of 3,100,000 sq km, draining almost 20% of the South American continent. Of all the rivers that form the Prata River Basin, the Paraguay River is the one that runs deepest into the centre of the continent. Before its confluence with the Paraná river, it runs an extension of 2,612 km, 1,683 km of which is within Brazilian territory, with some sections shared with Bolivia and Paraguay.

The *Alto* Paraguay Basin comprises two areas with considerably diverse conditions regarding natural and water resources: the Plateau and the Plains (Figure 1). The Plateau is located on the north and east of *Alto* Paraguay hydrographic basin. It is a relatively high altitude area, with datum levels above 200 m, sometimes reaching 1,400 m, located in the basin's eastern region, almost entirely within Brazilian territory, where drainage is well defined and converging. The Pantanal, one of the main biomes in South America, is located in the lowlands, also comprising flood-prone areas in Bolivia and Paraguay.

The Pantanal is a lowland area, located in the centre of the basin, where the rivers flood the plains and feed an intricate drainage system comprised of extensive lakes, diverging water bodies and seasonal drainage and flooded areas. The Pantanal region possesses datum levels ranging from 80 m to 150 m and was formed by the sinkage of a large area, which occurred simultaneously with the emergence of the Andes Mountain Range (Silva, 1984). The datum level of 200 m altitude corresponds, approximately, to the boundaries of the Pantanal lowlands, and the steep slopes, mountains and the Plateau's tablelands.

Finally, there is the *Chaco*, located west of the Brazilian border, which is a lowland area, where precipitation is below 1,000 mm per year, with large areas where river flow forms swamps or lakes, which rest without a defined drainage system.

While the fountainheads of the rivers that form the Pantanal have their origins in the highlands, with a predominant cerrado biome, and typical environmental, economic and social context of the cerrado, the flooded lowlands below, called Pantanal, have their own unique characteristics of seasonably flood-prone areas.

It must be noted, for instance, that roughly the same amount of water that comes from local precipitation in the Pantanal is lost through evapotranspiration. Thus, the regime of flooding and draining, which is fundamental for the functions of the natural system, relies fundamentally on the cerrado portion – the fountainheads on the highlands, a vital fraction in the BAP for the Pantanal.

From the perspective of ecosystem function, the crucial element for the functioning of the Pantanal system in the relationship between plateau and lowlands, is the hydrologic flow that creates feeding and reproductive niches for the regional biodiversity. Because of those characteristics, the Cerrados/Pantanal system is considered one of the biodiversity and water resources hot-spots in the planet, for its importance and for the degree of exposure to environmental threats.

The lowlands are formed by the tributaries on the left bank of the Paraguay River, within Brazilian territory, with its western border touching the territory of Bolivia to the north and Paraguay to the south (Figure 2).

The plateau's fountainheads feed different basins, in accordance with slope direction. The waters from the highlands at the extreme northern portion of Alto Paraguay Basin (Parecis and Cuiabá) flow toward the Amazon Basin on the northernmost side, and to BAP through the downward slope running towards south; the eastern slopes (Bodoquena, Maracaju and São Jerônimo) drain through

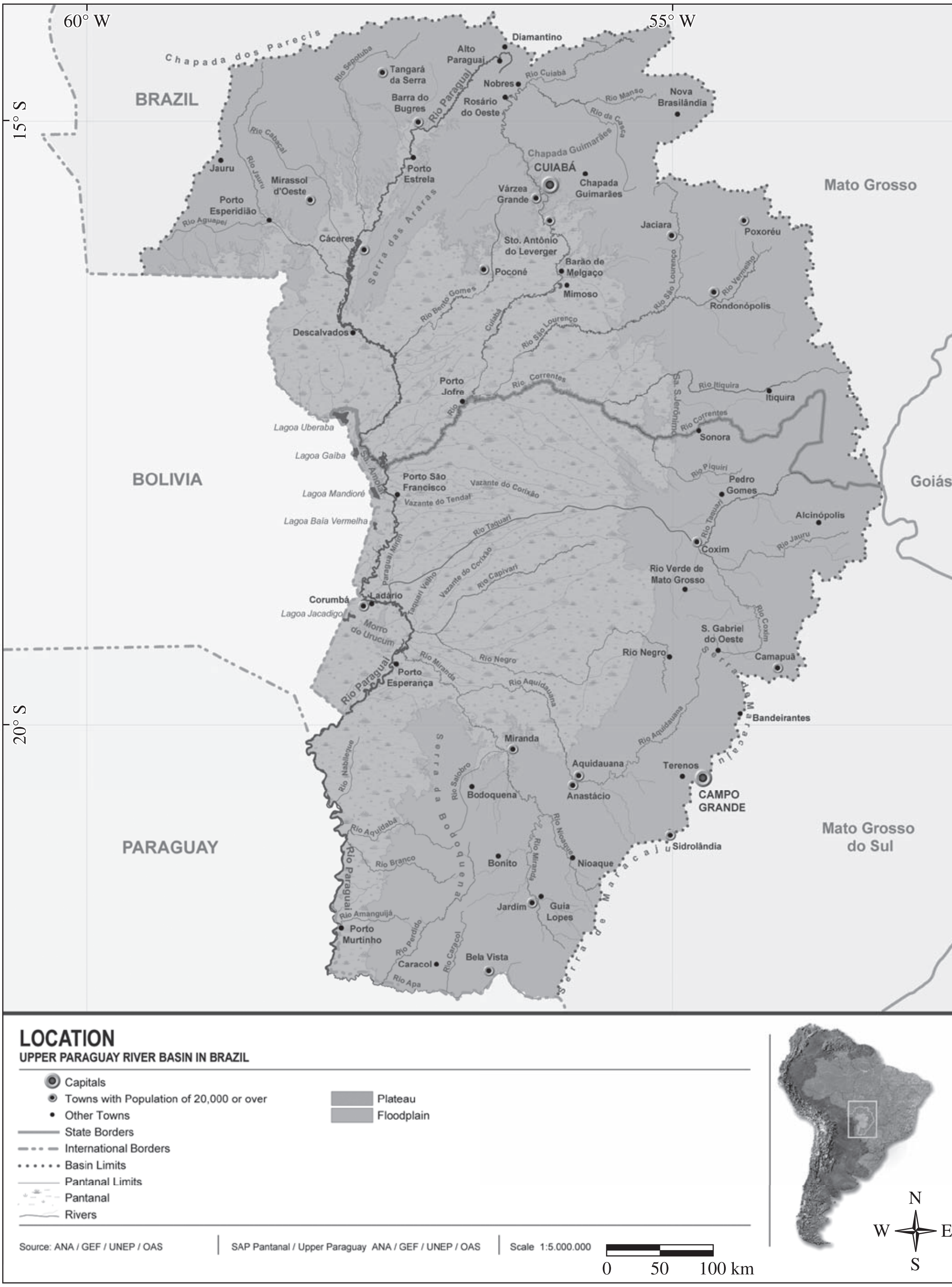

Figure 1. Location of the Pantanal/Upper Paraguay River in Brazil (ANA, 2004).

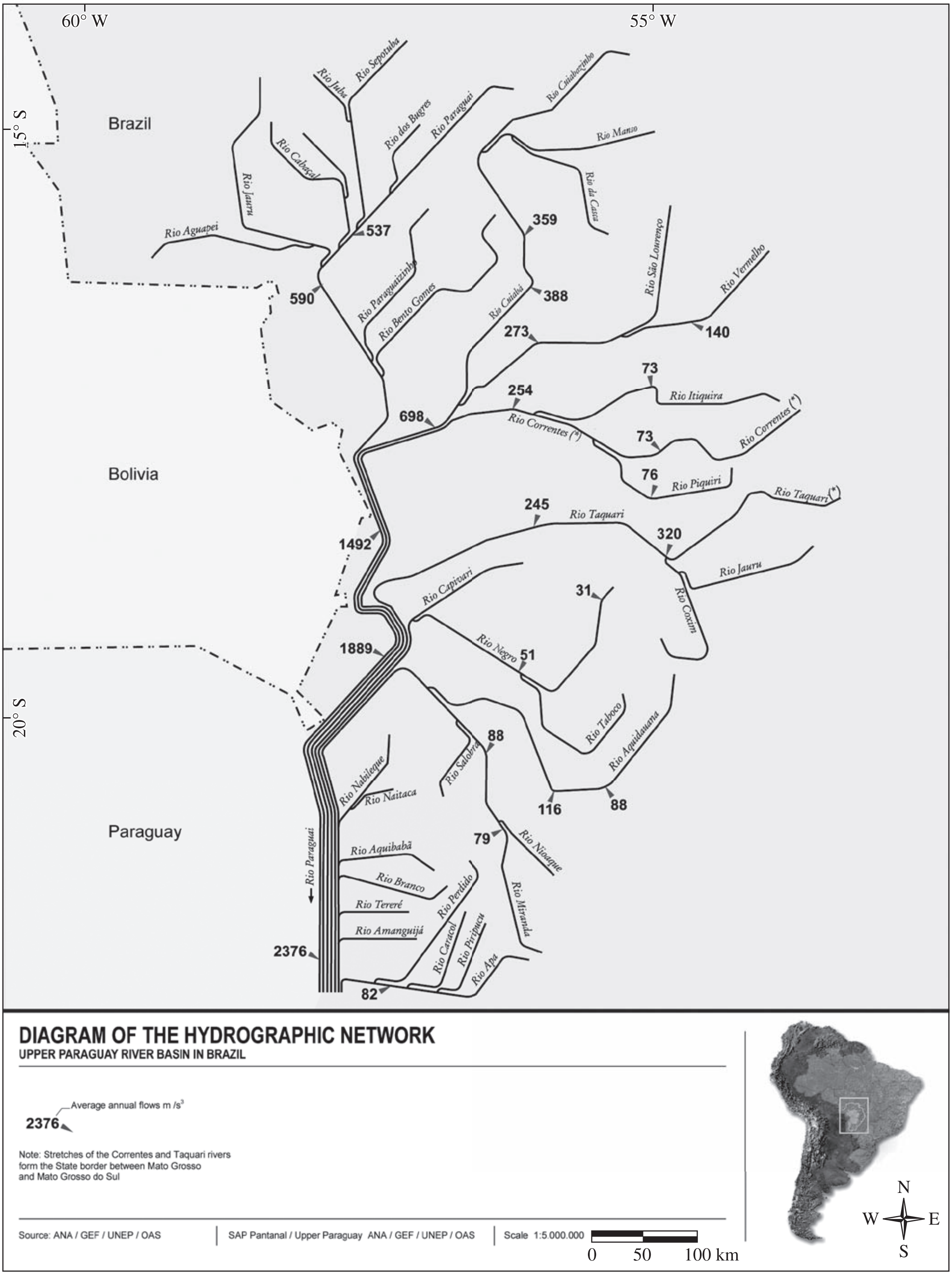

Figure 2. Upper Paraguay River Basin in Brazil - Diagram f the hydrographic network (ANA, 2004).

the eastern declivity towards Araguaia and Paraná rivers, and, through the western declivity they flow into the Alto Paraguay Basin.

The main rivers running down from the highlands into the plains are: from north to south, Paraguay, Bento Gomes, Cuiabá, São Lourenço - Itiquira, Taquari, Negro, Aquidauana - Miranda, Nabileque and Apa rivers.

When the flat surfaces meet the plains, they slow down the water flow in the riverbeds and during the rainy season, the rivers overflow their banks, thus flooding the lowlands.

In general, river declivity in the plateau is 0.6 m/km while declivity on the plains varies from 0.1 to 0.3 m/km. The depressions get filled with water, forming the baías, which are channels linking flooded valleys, shaping the channels (corixos); and shallower depressions interconnect the flooded areas, forming the drainage ditches.

The Basin does not boast a wide climate variation and may be wholly classified as a tropical humid climate. Average annual temperatures vary between 22.5 °C and 26.5 °C. The hottest month is November (with an average temperature of 27 °C) and the coolest is July (with an average temperature of 21 °C).

Average annual precipitation in the Basin is 1,396 mm, ranging from 800 mm to 1,600 mm, and the heaviest rainfall occurs in the Plateau region. The rainy season is from October through April and the other months make up the dry season. Average annual evaporation is 1,239 mm, with peaks in August, when higher rates of insolation are observed (Figure 3).

The average water flow in the Basin was 2,464 m^3/s, at the confluence with the Apa river, in the period 1939-2002 (Figure 4). The Pantanal acts as a great reservoir, retaining the largest share of the waters originated from the Plateau, thus regularising the flow from Paraguay River during up to five months, between inflows and outflows. In Cáceres, the greatest average flow happens in March, at the end of the rainy season; in Porto São Francisco, it occurs in April and May; in Porto Murtinho the flow is greater in June and July, entirely outside the rainy season. In the Plateau, the specific flows reach 13/18 l/s/ sq km and, in the Pantanal, in general, they are less than 0.5 l/s/sq km. Table 1 shows the average monthly and annual flow in the Pantanal and Alto Paraguay Basin (ANA, 2004).

On the northern portion of the Pantanal, the relative contribution of the tributaries coming down from the plateau accounts for 72% of the flows running into the Paraguay River. For the southern Pantanal, it corresponds to 28%.

The northern portion of the Pantanal receives contributions from: Alto Paraguay - 27%; Alto and Médio Cuiabá - 20%; São Lourenço - 14%; Correntes-Itiquira-Piquiri - 11%.

The contributions in the southern portion of the Pantanal come from: Alto Taquari - 16%; Negro - 3%; Alto Aquidauana - 5% and Alto Miranda - 4%. It should be noted that the Basin's declivity in the plateau is 30 cm/km on average, and in the Pantanal it is 3-5 cm/km, running from east to west and 1.5 to 3 cm/km in the north-south direction, towards the Paraguay River.

In the Pantanal, the flooding area of the alluvial fans has an average expanse of 50,000 km^2 (Figure 5). Ladário is the reference fluviometric station in the Brazilian Pantanal. The station has been monitored by the Brazilian Navy since 1900. When the maximum annual level in Ladário reaches or exceeds 4 m, it is considered that there is flooding in the Pantanal; When the level varies between 4 and 5 m, the flood is light; between 5 and 6 m, it is considered normal and above 6 m, it is deemed a severe flood. In years of very intense rainfall, such as 1988 (6.64 m, the greatest historical mark) and 1995 (6.56 m, third greatest mark in the century), the Paraguay River, in the Pantanal, overflows its banks by flooding and expands to a width of 20 km. Land submersion depth in the Pantanal ranges from 0.5 m to 1.5 m in average. Submersion duration varies greatly. In some areas the floods may last up to six months. The floods confined in the sub-basins do not have a direct influence on the Pantanal floods.

The low drainage capacity of the rivers and lakes that form the Pantanal, coupled with the region's climate, produce intense evaporation. Approximately 60% of all the waters originated from the Plateau are lost through evaporation.

The current knowledge of the conditions of the Alto Paraguay Basin, in terms of surface water availability and demand, indicates that the greatest demand in the entire Pantanal/Alto Paraguay Basin is destined to animal drinking. The greatest demands for irrigation are located in areas of the Miranda, Itiquira and Correntes rivers sub-basins. The greatest urban and industrial demands are located in the Alto and Médio Cuiabá river basins. Those demands are relatively small (3.5%) as compared to the average water availability. It should be noted, however, that urban and rural water supply in the Pantanal/Alto Paraguay Basin makes widespread use of water collection from shallow and deep wells.

The Alto Paraguay Basin, including Pantanal, while boasting an abundant availability of water resources, also presents some conditions of scarcity in some sub-basins and different periods of the year, due to the hydric balance or the observed use.

The rivers in the region have the capacity to convey the average discharges, but during the flood season, they inundate extensive areas of lowlands, forming temporary lakes that take up a total area of roughly 100,000 sq km. In early May, the water level starts to slowly go down, and the area becomes characteristically swampy. When the lowlands dry up, the soils are covered with a thin layer of nutrients that fertilise the grasslands that feed a herd estimated in three million heads.

As for underground waters, the basin's largest portion is made up of porous aquifers associated with non consolidated sediments that cover ancient rocky substratum. The underground aquifers are located at an average depth of 50 m and their discharge exceeds an average of 30,000 L/h. there is an abundance of underground water in the Pantanal, but there is some evidence of potential forthcoming problems with water quality, in terms of salinity and the presence of heavy metals. In general terms, the quality of water

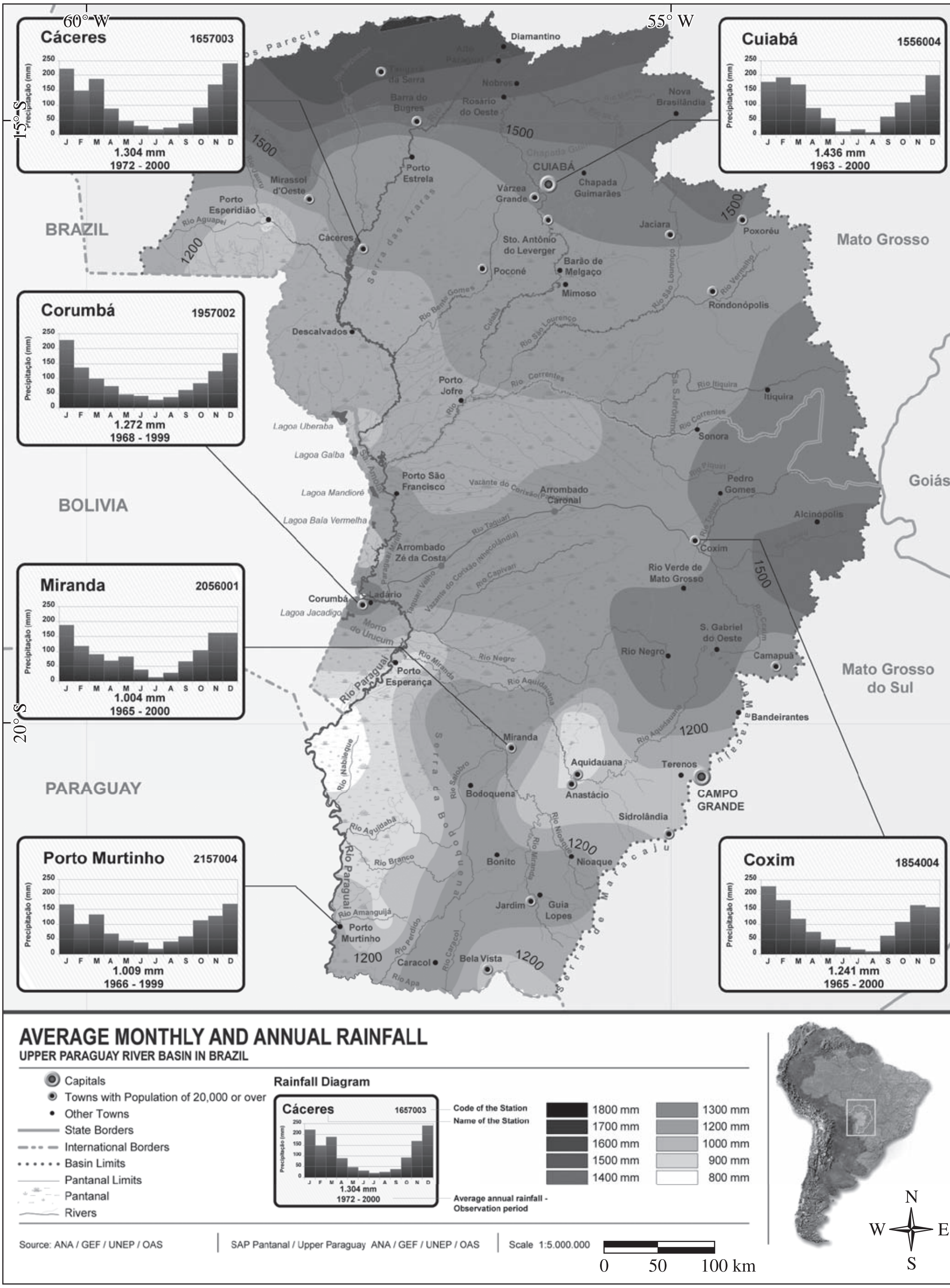

Figure 3. Upper Paraguay River Basin in Brazil – Average monthly and annual rainfall (ANA, 2004).

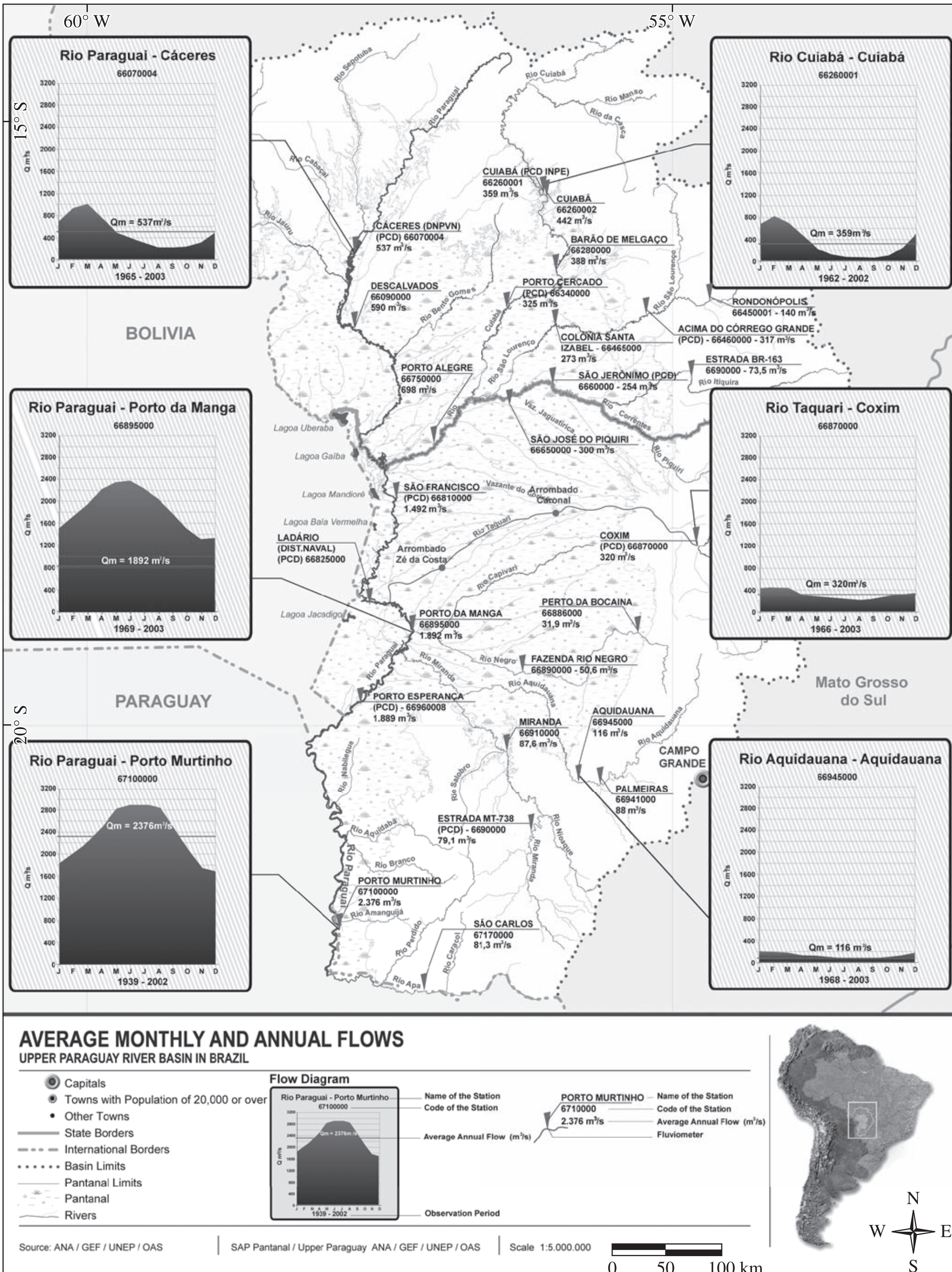

Figure 4. Upper Paraguay River Basin in Brazil - Average Monthly and Annual Flows (ANA, 2004).

Table 1. Pantanal and Alto Paraguay Basin average monthly and annual flows.

River and station name	Code and area (sq km)	Average monthly flows in m^3/s												Annual average flow Q_{95} (m^3/s)	Observation period
		J	F	M	A	M	J	J	A	S	O	N	D		
Paraguay	66070004	753	932	1.010	799	565	400	314	268	262	279	343	521	**537**	1965/
Cáceres	32,774													180	2003
Paraguay	66090000	738	830	869	831	714	558	439	365	348	367	447	590	**590**	1967/
Descalvos	**48,360**													229	2003
Cuiabá	66260001	698	808	745	451	243	155	124	107	114	158	246	464	**359**	1962/
Cuiabá	**23,226**													64	2002
Cuiabá	66280000	717	810	832	596	382	199	144	132	142	178	262	521	**388**	1966/
Barão de Melgaço	**27,050**													84	2002
Vermelho	66450001	287	317	279	190	112	84.3	70.1	6.3	68.7	84.6	119	217	**140**	1965/
Rondonópolis	**11,995**													35	2003
São Lourenço	66460000	517	550	571	441	301	227	180	155	165	188	260	407	**317**	1969/
Córrego Grande	**21,800**													117	2002
Itiquira	66525000	104	113	110	84.3	68.6	57.1	49.2	43.6	45.6	51.9	65	82.9	**73.5**	1969/
Estrada BR-163	**5,100**													26.2	1981
Correntes	66490000	92.7	97.6	98.1	88.7	79.6	74.1	69.2	65.9	67.5	69.8	78.3	86	**76.2**	1969/
Estrada BR-163	**3,030**													45.2	2003
Piquiri	66600000	351	400	422	354	261	210	178	154	152	163	188	525	**254**	1967/
São Jerônimo	**17,150**													101	2003
Cuiabá	66750000	811	936	974	961	876	731	567	459	425	456	537	659	**698**	1967/
Porto Alegre	**102,750**													321	2003
Paraguay	66810000	1,048	1,335	1,950	2,267	2,229	1,991	1,708	1,420	1,198	1,028	940	940	**1,492**	1967/
São Francisco	**243,000**													638	2003
Taquari	66870000	438	479	433	343	294	267	248	238	248	278	316	373	**320**	1966/
Coxim	**27,040**													142	2003
Taquari	66885000	271	279	280	269	258	248	239	229	225	241	250	261	**245**	1968/
Porto Rolom	32,285													128	1993

Source: ANA (2004).

Table1. Continued...

River and station name	Code and area (sq km)	Average monthly flows in m^3/s												Annual average flow Q_{95} (m^3/s)	Observation period
		J	F	M	A	M	J	J	A	S	O	N	D		
Paraguay Porto da Manga	66895000 **316,000**	1.502	1.716	1.927	2.210	2.331	2,363	2,222	2,027	1,772	1,500	1,312	1,332	**1,892** 815	1969/ 2003
Negro Fazenda Rio Negro	66890000 **14,770**	129	119	121	80,3	66.5	57.4	32.6	16.2	12.6	23	38	76,1	**50.6** 2.8	1968/ 1986
Aquidauana Aquidauana	66945000 **15,200**	188	178	164	117	110	86.7	66.4	59.1	66.2	85.1	112	162	**116** 32.3	1968/ 2003
Miranda Miranda	66910000 **15,460**	155	144	118	90.4	80.5	76.8	47	40.2	46.1	63.4	87.9	134	**87.6** 16.7	1965/ 2003
Paraguay Porto Esperança	66960008 **363,500**	1,485	1,792	2,053	2,345	2,438	2,402	2,246	1,982	1,768	1,538	1,327	1,290	**1,889** 1,053	1963/ 1981
Paraguay Porto Murtinho	67100000 **474,500**	1,827	2,008	2,266	2,506	2,818	2,989	2,999	2,871	2,566	2,145	1,776	1,701	**2,376** 903	1939/ 2002
Apa São Carlos	67170000 **11,100**	128	102	90.8	73.6	88.7	77.5	37.3	39.2	40.4	57.3	101	153	**81.3** 4.8	1971/ 2002

Source: ANA (2004).

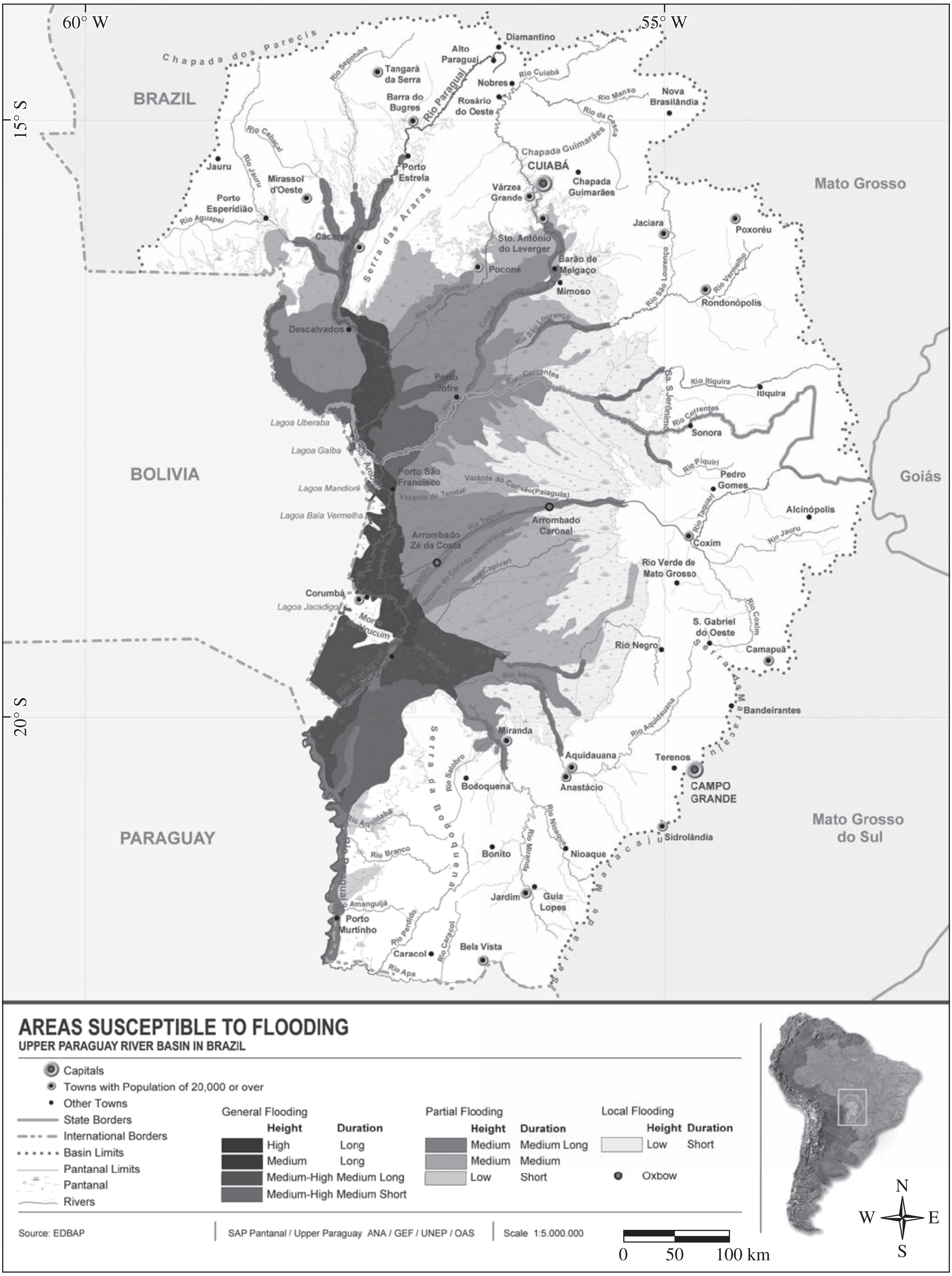

Figure 5. Upper Paraguay River Basin in Brazil – Areas susceptible to flooding (ANA, 2004).

in the plateau may be considered good, although water availability is somewhat more restricted to some areas.

The Pantanal regulates river discharge through periodical flooding. It hoards the waters and also stimulates water loss through evapotranspiration and soil infiltration. The river sediments are retained during the passage of river waters through the Pantanal with the consequent transformation of solutions and biogeochemical elements that are important for the biodiversity in the region.

4. The Natural System and its Functioning

4.1. Dynamics of inundation

Hydrology in the Pantanal is irregular: even being seasonal, the flood periods vary throughout the plains, due to the volume of water flows running into the lowlands and to the smooth and flat declivity of the terrain. The flood periods may be delayed after rainfall on the riverheads in the plateau, due to the slow passage of the waters through the flooded plains. A great portion of the Pantanal is flooded by river discharge, which overflows their banks when they reach the Pantanal, but in some specific spots, the local rainfall may also produce shallow floods. During the period of high water levels, the water flows move slowly through the Pantanal, interconnecting the rivers with the depressions, through canals and drainage ditches, filling up the flood-prone areas. The water level at the Paraguay River channel in Ladário is close to 6 m and approximately 2 m in the portion where the river overflows in the plains.

The Paraguay River runs from north to south along the western part of Pantanal, and receives water from its tributaries, particularly the ones located on the left bank. River declivity in the Pantanal is 2.5 cm per km (EDIBAP, 1979) and there is the presence of large lakes along the river, with close hydrologic relationship with the Paraguay River, which has a sinuous shape in the Pantanal portion. Those lakes are: to the south of Corumbá, Jacadigo Lake; to the north of Corumbá, we find Baía Vermelha, Lagoa Mandioré, Lagoa Guaíba and Lagoa Uberaba. Past the city of Cáceres, the river declivity ranges from 6.3 cm km-1 to 1 cm km-1 near the Apa River (Carvalho, 1986).

After receiving a strong influx of water in its riverheads, the Paraguay River supplies water to the flood-prone areas of the Pantanal, but the flood wave may be delayed by four to five months until it reaches the southern portion of Pantanal. Thus, the changes in water levels show that there is a delay of approximately four months before the water level passes through the Pantanal, from north to south, and reaches the city of Corumbá. During this period, when water levels reach their peak in Corumbá, the dry season is already underway in the northern Pantanal (Hamilton et al., 1996).

In the city of Corumbá, the Paraguay River annual discharge is 1,260 m^3/s-1 (cubic metres per second) when the river accounts for 80% of the flow in the region (EDIBAP, 1979). While the National Water Agency (ANA, 2004) estimates that the Paraguay River discharge in Porto Murtinho is 2,376 m^3/s-1, other estimates show a discharge of 2,500 m^3/s-1 in Corumbá (Hamilton et al., 1997).

Hydrologic data show that there are marked differences between the northern and southern portions of Pantanal: the flood regime and flood fluctuation is greater in the north. However, the physical and chemical conditions of the waters in the southern portion of the Pantanal are more stable than in the northern portion, since the north is drier in the dry season. Peak discharge from the tributaries occurs earlier than the Paraguay River discharge, and the subsequent elevation of the Paraguay River waters block the flow of its tributaries (Hamilton et al., 1996). As mentioned before, the flood peaks produced by the Paraguay River discharge in the south occurs four months later than rainfall peaks in the riverheads, so the floods are mainly caused by river overflow and not by rainfall (Hamilton et al., 1996).

The largest flood-prone areas are located along the Paraguay River, between Porto Conceição and Porto Murtinho, reaching depths of 1 m to 1.5 m. Those floods may last for up to six months. In the other areas of the Pantanal, submersion of the flood-prone areas has a depth of roughly half a metre and the flood duration varies from region to region. In the area of Paraguay and Jauru rivers, it lasts approximately 70 days; in Cuiabá, Aquidauana-Miranda, it lasts roughly 40 days and in Taquari and São Lourenço rivers, the duration is about 30 days, according to data from PCBAP (1997a). In the portion of Pantanal that receives water from the Negro and Taboco rivers, the flood may reach 1.2 m and last up to 90 days. The flood-prone area measures approximately 300 km by 400 km, and may reach a total area of approximately 137,000 sq km, mostly within Brazilian territory and some small sections in Bolivia and Paraguay (Hamilton et al., 1996, 1997).

Long-range studies show that the flood pattern in the Pantanal varies from February, in the north, through June, in the south, as a result of the drainage delay in the region (Hamilton et al., 1996, 1997). During nine years of observations, an area of 131,000 sq km was flooded, between 1979 and 1987. The estimates for total monthly flooded areas vary between 11,000 and 110,000 sq km.

4.2. Seasonality and yearly cycles

There are very pronounced seasonal floods in the alluviums of Taquari, with peaks occurring in February. This demonstrates the inter-annual variability in maximum and minimal levels of the flooded areas (Hamilton et al., 1998). The water influx from the river Taquari has its peak one or two months after rainfall peak in the region. Thus, the floods may be a result of that influx and also of local rainfall. After March, the water deficit is explained by the evapotranspiration of the flooded area.

The areas where the Taquari river fountainheads are located have an erosive potential, but are protected by natural plant cover. With the advent of deforestation, the erosion became more severe, producing the so-called arrombados of the Taquari River in the Pantanal. Arrombados are fissures in the river bank caused by intense siltage in the riverbed. Such alteration has provoked changes in the seasonal flooding regime and transformed areas that were only periodically flooded in areas of permanent inundation, currently estimated to occupy an area of 11,000 sq km (ANA, 2004).

In northern Pantanal, the floods occur between March and April, while in the south they take place from July to August. Between November and March there is intense water loss due to evapotranspiration. The heaviest rainfall occurs from October through March. The river flows (m^3s^{-1}) have their influx from January through April, with peaks in March and the discharges occur from April through October, with peaks in June-July, measured in Porto Esperança, on the Paraguay River (Hamilton et al., 1997).

Maximum seasonal flood in the region occurs between February and April, and declines, with peak dry weather between October and December. Besides the annual floods, there are variations in longer periods of time, with no defined pattern. Such floods are influenced by several factors, in both the macro and micro scales. The river level variations rely fundamentally on the precipitation characteristics each year. The river level is an indicator of two important variables: drainage and size of the river canal, including the adjacent area.

The slow flow of waters in the Pantanal is a determinant factor for the loss of sediments in suspension, and contributes to the drop of dissolved oxygen levels and decreased pH.

Statistical treatment of data from the hydrometric station in Ladário, in the period 1900-1996, identified seven categories of floods, in an attempt to establish a methodology for a system of flood alert (Adamoli, 1996). During that period, the critical level of four metres of river depth was exceeded in 61 out of the 97 years of observation recorded in Ladário. In some years, there were severe floods, when the water level exceeded 6 metres (in the years 1905, 1913, 1920, 1921, 1980, 1981, 1983, 1986, 1989, and 1995). In contrast, there were dry years, with river levels below two metres (1910, 1911, 1915, 1938, 1939, 1941, 1944, 1948 and from 1964 to 1973). In the period 1961 to 1973 there was diminished precipitation, and the extent of variations in the Paraguay River also declined, as detected by different methods (Sá et al., 1998). From then on, there was a considerably more humid period, from 1974 to 1996.

Such hydrologic seasonability, with an annual hydraulic pattern, is ecologically decisive for wildlife survival in Pantanal.

5. Hydrologic Behaviour

The data obtained from Ladário measurements are fundamental if one needs to get a full grasp of the hydrologic behaviour of the Paraguay River in the BAP section. That fluviometric station possesses a vast series of levels. Moreover, the station controls approximately 81% of the average water outflow from the Brazilian territory (ANA, 2008).

The Paraguay River's fountainheads are located in the complex of the Parecis Mountain Range, close to the city of Diamantino in the state of Mato Grosso. It drains the Pantanal, together with its tributaries. In the BAP, Paraguay River expands and forms a damming zone, and becomes the main tributary of BAP, that comprises two distinct regions: the Plateau and Pantanal.

Valverde (1972) considers three factors as preponderant for the regularity of the Paraguay river's fluvial regime: periodic annual rainfall with maximum regularity, falling on the basin, especially on the upstream tributaries; extensive flooded and damming zone in the Pantanal, which feeds the system during the dry season and smooth slopes in the longitudinal section and a great uniformity in the gradient, from São Luis de Cáceres up until the mouth of the Paraguay River.

Those considerations are evidence of the conjugated action of several factors in the hydrologic behaviour of the water bodies.

The upstream course of the Paraguay River in the Plateau corresponds to the fountainhead area, or mountains and depressions, and because of that, the river has rapids and a declivity equivalent to 75 cm/km. One may observe that the riverheads have a quick response to precipitation, with peak flows in the rainy season. In the plains and Pantanal, however, the average annual flow peaks occur in the dry period. This is due to the basin's characteristics, which has an intricate drainage system, with large flood-prone areas that act as reservoirs.

Thus, the Paraguay River presents a typical regime of single mode tropical inundation in the portion where the Ladário station is located (Catella, 2001; Soares et al., 2008) or else, each year the river level in Ladário (MS), presents one single phase of ascent (growth), reaching the peak of flooding, and a single phase of descent (recession), not considering the little "bursts" that occur in the low water season (Galdino and Clarke, 1995, 1997).

The phase of rising waters is called inundation and the lowering of waters is called leaking. Transitions between periods are called floods, when the river reaches its peak level, and drought when it reaches minimum level. With those figures in hand it is possible to characterise a period as either dry or flooded in Pantanal (ANA, 2008).

In 2006, Ladário station registered a level of 5.40 m, and it was considered by Soares et al. (2008) as the highest flood peak since 1997. According to the authors, in the same year, during the phase of drying up, the levels observed were above the historical average, and the minimum datum attained (2.16 m in 6 December 2006) was also the highest since 1992.

However, in spite of the large volume of water hoarded up in the surface or underground reservoirs of the Pantanal in the floods of 2006 and 2007 (Soares et al., 2008), the Ladário station registered, during the outflow of 2007, one of the lowest minimum levels of the last 34 years, that is 88 cm on 3 November 2007.

In accordance with the classification by Galdino et al. (2002), the flood in the hydrologic period 2007-2008, as well as the floods of the two previous years, may be considered "normal", that is, when the maximum water level in Paraguay River ranges between 5.00 and 5.99 m in Ladário.

According to a bulletin from the National Water Agency (ANA, 2008), in early 2008 the pluviometric precipitations were above the historical average in practically the entire BAP.

Total rainfall in January and February exceeded the historical average in 40% and 60%, respectively. The increased local rainfall contributed to a quick rise of the river water levels in the beginning of the flood period (end of 2007 and beginning of 2008).

Climate conditions on their own are not sufficient to explain the differences observed in the Paraguay River regime and some of its tributaries. The complexity of the hydrologic regime of the Paraguay River are related to the smooth declivity of the terrain comprised by the lowlands and marshlands in Mato Grosso (between 50 and 30 cm/km in the east-west direction and 3 to 1.5 cm/km from north to south). It is also owed to the area's extension, which remains periodically flooded, with a great volume of water. The river's sinuous course and the numerous geographic features outcropping in the flooded plains contribute to the sluggishness of water flows.

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Aquatic macrophyte diversity of the Pantanal wetland and upper basin

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(With 1 figure)

Abstract

This is a short review of the state of the art concerning diversity of aquatic macrophytes and the main aquatic vegetation types in the Brazilian Pantanal wetland and upper watershed. There are *ca.* 280 species of aquatic macrophytes on the Pantanal floodplain, with scarce endemism. On the upper watershed, *Cerrado* wetlands (*veredas*) and limestone springs have a distinct flora from the Pantanal, with twice the species richness. As a representative case of aquatic habitats influenced by river flood, some primary data are presented for the Pantanal Matogrossense National Park and associated Acurizal Preserve, analysing the floristic similarity among aquatic vegetation types. We comment on problems of conservation and observe that *Panicum elephantipes* Nees is one of the few natives to compete with the invasive *Urochloa arrecta* (Hack. ex T. Durand & Schinz) Morrone & Zuloaga.

Keywords: flora, aquatic plants, floodplain, savanna, vereda.

Diversidade de macrófitas aquáticas do Pantanal e alta bacia

Resumo

Esta é uma breve revisão sobre o estado do conhecimento sobre as macrófitas aquáticas e os principais tipos de vegetação do Pantanal brasileiro e da alta bacia. A flora da planície inundável é de aproximadamente 280 espécies, com escasso endemismo. Na alta bacia, as áreas úmidas do Cerrado (veredas) e nascentes em calcário têm flora distinta do Pantanal, com o dobro da riqueza de espécies. Como um caso representativo de ambientes aquáticos influenciados por inundação fluvial, são apresentados alguns dados primários do Parque Nacional do Pantanal mato-grossense e da Reserva Acurizal associada, analisando-se a similaridade florística entre tipos de vegetação aquática e comentando-se os problemas de conservação na região, onde foi observado que a espécie *Panicum elephantipes* Nees é uma das poucas nativas que competem com a invasora *Urochloa arrecta* (Hack. ex T. Durand & Schinz) Morrone & Zuloaga.

Palavras-chave: flora, plantas aquáticas, campo úmido, savana, vereda.

1. Introduction

The first botanical reports on aquatic plants of the Pantanal come from European naturalists who crossed the region, as summarised by Sampaio (1916). Foremost among Brazilian botanists was the pioneering Hoehne (1923), who collected in the Pantanal, looking closely at aquatic plants, many of them mentioned in his book (Hoehne, 1948).

Then a gap occurred up until the last two decades, when local botanists started to give some information on the regional flora (e.g. Pott and Pott, 1994, 1997). Various surveys on aquatic macrophytes of the sandy Pantanal, flooded by rain, have been previously reported (e.g., Pott et al., 1999). Some as yet unpublished data on the Pantanal Matogrossense National Park are presented, gathered by the authors and extracted from the Rapid Ecological Assessment-Botany report (Pott et al., 2001), as a representative case of aquatic vegetation influenced by river flood.

2. Results and Discussion

2.1. Flora

Diversity of aquatic macrophytes in the Pantanal varies from the smallest (*Wolffia brasiliensis* Wedd.) to the largest hydrophyte, *Victoria amazonica* (Poepp.) Sowerby. There are at least 280 species of aquatic macrophytes in the Pantanal (Pott, 2008), most of them shown in the identification manual by Pott and Pott (2000), considering various degrees of dependence on water. The most numerous families are Poaceae (26), Cyperaceae (19), Fabaceae (15), Onagraceae (15) and Pontederiaceae (12), and the best represented genera are *Ludwigia* (15), *Bacopa* (12), *Utricularia* (11), *Nymphaea* (7), and *Polygonum* (7) (Pott and Pott, 2000; Pott, 2008).

Taxonomic work on aquatic plants in the Pantanal is as yet restricted to a few groups, such as Nymphaeaceae (Pott, 1998), Araceae-Lemnoideae (Pott and Cervi, 1999), *Aeschynomene* (Lima et al., 2006), and some genera have been reviewed on a Brazilian scale, such as *Panicum* (Guglieri and Longhi-Wagner, 2004). World-wide reviews such as *Utricularia* by Taylor (1989) are also very useful.

Research on macrophyte vegetation has been carried out mainly in floristics. It is often concentrated on a few spots, e.g., Pott et al. (1989, 1999) at Nhumirim ranch (Nhecolândia), Costa (2004) at Santa Emília ranch (Aquidauana), Nunes da Cunha et al. (2000) at Pirizal (Poconé) and other areas of Poconé (Prado et al., 1994; Schessl, 1999).

Cerrado wetlands (*veredas*) on the upper watershed and close by headwaters of the Paraná basin have a richer flora, with at least 574 species (Pott, 2008), twice the species richness found in the Pantanal. The flora of limestone springs on the Bodoquena upland is not very diverse but forms attractive underwater gardens (Pott, 1999).

Many aquatic plants which occur in the Pantanal are elements of wide distribution, in common with wetlands in other neotropical phytogeographic provinces, such as Amazonia and the Paraná basin. *Veredas* contain many additional Poaceae, Cyperaceae, Melastomataceae, etc., in common with other wet grasslands of South America.

There are floristic dissimilarities between the plain and the upper watershed (Pott, 2008), for example, in the crystalline streams of Bonito (Bodoquena range) grows *Potamogeton illinoensis* Morong (Pott, 1999), not yet found in the Pantanal, whereas the giant waterlily *V. amazonica* has exclusive occurrence in oxbow lakes of the lower floodplain (Pott, 2008). Also unique in Mato Grosso do Sul is the wetland sawgrass *Cladium jamaicense* Crantz (Pott, 2008), with *Chara rusbyana* M. Howe covering gaps, on organic soil upon sedimentary calcium carbonate. However, floristic similarity of the Pantanal with wet grasslands of the upper basin increases towards the *Cerrado* uplands, on the eastern sandy soil, with species in common such as *Drosera sessilifolia* A. St.-Hil., *Echinodorus grandiflorus* (Cham. & Schltdl.) Micheli, *Xanthosoma striatipes* (Kunth & Bouché) Mad., etc. Nevertheless, the grass-sedge community of *Mauritia* (*M. flexuosa* L. f.) palm wetlands in the headwaters and along *cerrado* streams of the upper basin is quite distinct from this palm formation on the plain (Pott, 2008), where it only occurs along a few rivers (Aquidauana and Taquari) (Silva et al., 2000) and is associated with species of seasonally flooded grassland or riparian scrub quite different from *veredas*.

Often there are large areas with assemblages dominated by a single macrophyte, such as species of *Oryza* and *Polygonum*, generally with strong vegetative propagation, or various communities may occur within a short distance. Some hydrophytes survive the dry season as dormant rhizomes, which is the case of *Echinodorus* spp., *Eleocharis* spp., *Nymphaea* spp., *Sagittaria* spp.. These are therefore among the first to reappear in the wet season, while others grow from seeds (*Ludwigia* spp.) and spores (*Salvinia*), and many use both vegetative and reproductive strategies. Year-round water level may vary up to 7 m in the river system, while fluctuation is much less in non-coalescent isolated ponds and most areas flooded only by rain. Flood cycles can be drawn from daily records taken by the Navy since 1900 at the hydrometric station at Ladário.

Some species are associated with lotic habitats, such as *Ludwigia inclinata* (L. f.) P.H. Raven, *Nymphaea oxypetala* Planch., but more often with lentic environments, while some occur in both, like *Eichhornia azurea* (Sw.) Kunth. Most sub-regions do not have lakes and ponds, and therefore have quite a monotonous landscape, compared to Nhecolândia, Rio Negro (part of Aquidauana) and Abobral, which present high diversity of habitats, such as brackish and fresh water ponds, seasonal streams, floodplain channels and ancient river beds ("corixos") and anabranches. Brackish ponds ("salinas") are poor in macrophyte species, where only *Paspalum vaginatum* Sw. and charophytes occur. Along the Serra do Amolar there are large lakes (Vermelha, Uberaba, Mandioré, Gaíva, etc.), with aquatic vegetation restricted to shores and wind-sheltered inlets.

2.1.1. Endemic and rare species

The Pantanal is a Quaternary floodplain, geologically recent (Holocene), so very few endemic species occur, none of them aquatic. However, the endemic peanut *Arachis vallsii* Krapov. & W.C. Greg. can be considered aquatic, as it grows in 40 cm flooded mud under *Copernicia alba* Morong, on the floodplain of Lake Baía Negra and in a few other clayey spots, where it flowers and sets fruit, with the advantage of its long hollow peg and stem, characteristic structures of aquatics. A few species are quite rare or show very restricted occurrence, such as *Nymphaea belophylla* Trickett, *Eichhornia diversifolia* (Vahl) Urb., *Oryza grandiglumis* (Döll) Prod., found near the Paraguay River in Cáceres, *Discolobium psoraleaefolium* Benth., collected only on the eastern part of the alluvial fan of the Taquari River. For instance, *Eulophia alta* (L.) Fawc. & Rendl. has been found on an old floating island, *Xanthosoma aristiguietae* (Bunting) M. Madison, on the margins of the Miranda River to where rooting stems could have been carried in pre-Columbian times as a medicinal plant.

2.2. Life forms

Aquatic macrophytes have been grouped according to their life form, into submerged, free floating, rooted floating, emergent and amphibious (Irgang et al., 1984), and epiphyte (Tur, 1972). Usually life form zoning occurs according to water depth: amphibians on the littoral, emergents on the shallow belts, and others in the deeper zones (Pott et al., 1989).

2.3. Types of aquatic habitats and main vegetation types

According to Silva et al. (2007), there is a total of 2,557 km^2 of open water in the dry season of the Pantanal, considering only that with a vegetation-free surface. However, the flooded area varies from 7 to 70% of the Pantanal, so at high flood it may reach 110,000 km^2, according to Hamilton et al. (1996), who used radar images, so also taking into account floating aquatics.

Floating mats ("camalote") and floating meadows ("baceiro", "batume") are both found in permanent water bodies such as ponds, lakes, canals, oxbows and rivers. The floating aquatic "batume" was defined by Da Silva (1984). Floating mats are attached banks of floating macrophytes, or they may not be anchored, so that they float downriver or may be driven by wind; the main species of these are the water hyacinths *Eichhornia crassipes* (Mart.) Solms and *E. azurea* (Sw.) Kunth, then both can be uprooted and become free-floating. On top of them and on free-floating aquatic plants (water lettuce, *Pistia stratiotes* L., water fern *Salvinia auriculata* Aubl.), *Oxycaryum cubense* (Poepp. & Kunth) Palla starts to grow, with densely entangled long hollow roots and rhizomes, and gradually the floating mats become floating meadows, with denser vegetation, made up mainly of *Eleocharis plicarhachis* (Griseb.) Svenson, rooted on histosol, as long as the pond does not dry (Pivari et al., 2008). Histosol is a sort of organic soil made of decomposing plants (Neiff, 1978). As the floating meadow ages, the histosol thickens up to more than 1 m, allowing humans to walk on it, as we have already done with a group of 10 people. This floating vegetation is most frequent in the Western zones, in the sub-regions of Abobral and Cáceres and along the Paraguay, Cuiabá, Negro, Miranda and Nabileque Rivers. The cover of bursedge, *O. cubense*, mats can be distinguished on Landsat and SPOT images (Abdon et al., 1998).

Swamps ("brejos") or permanently flooded or waterlogged areas are not as common as the rather misleading toponym Pantanal (= swampland) may suggest, and are confined to wetter places and those with fine sediments, near rivers, such as the Negro (sub-region Aquidauana), which overflows and disappears into a wide swamp, and parts of the sub-regions of Abobral, Paraguay and Poconé. Also, lately the increasingly flooded Taquari delta has become a swamp, due to silting of the river bed and consequent permanent overflow (Pott and Pott, 2005). It contains grasses and sedges, often with some becoming dominant such as giant sedge *Cyperus giganteus* Vahl ("pirizal"), *Ipomoea carnea* var. *fistulosa* (Mart. ex Choisy) D.F. Austin ("algodoal"), fireflag *Thalia geniculata* L. ("caetezal") and cat-tail *Typha domingensis* Pers. ("taboal"), growing in swampy areas or temporary ponds. Cat-tail tends to increase in disturbed flooded areas and artificial ponds (borrow pits and dredged water holes for cattle), while *Rhynchospora trispicata* (Nees) Steud. and *Scleria variegata* (Nees) Steud. are very frequently found.

2.4. Annual cycle

Aquatic plants respond well to the flood dynamics. Many shallowly flooded grasslands dry up and the seasonal aquatics disappear, among them even perennials, such as *Pontederia parviflora* Alexander and *Sagittaria guayanensis* Kunth, as do small annuals like *Bacopa* spp. and *Echinodorus tenellus* (Mart.) Buch. A difference is that in the Pantanal there is a stronger wet and dry cycle, whereas on the upper watershed the flood pulse is much lower, even where there is 50-100% more rainfall. Here soils remain waterlogged or with a high water table all year round, fed by ground water in the dry season, flowing over an impermeable layer of laterite, making the water ferruginous, or over basalt or sandstone. Plant distribution in *cerrado* wet grassland and *vereda* is related to ground-water level (Meirelles et al., 2002), yet in the Pantanal the water table may fall below 2 m in the dry season, hence above-ground water level in the wet is a more important factor. In parts of the Pantanal, these changes in the dry and aquatic phases are more pronounced, reflected in a high proportion of opportunistic therophytes (Schessl, 1999), on intermediate ground between floodless and deep flooded stretches. *Vereda* soils are more organic and peaty, acting like a water storing sponge. These soils are organosoils and gleysoils (Ramos et al., 2006). The soils in the Pantanal, even though hydromorphic too, vary from pure sand to heavy clay, but due to the very flat landscape, in the dry period the water table reaches the surface only in depressed parts, for example in ponds and water courses.

2.5. Dynamics

Aquatic vegetation in the Pantanal changes over time, starting with free-floating plants such as *Salvinia* spp., *Pistia stratiotes*, and *Limnobium laevigatum* (Humb. & Bonpl. ex Willd.) Heine, which become colonised by the epiphyte *Oxycaryum cubense* (Pott and Pott, 2003) and later by *Eleocharis plicarhachis* (Pivari et al., 2008). In more permanent ponds and oxbow lakes, aquatic vegetation tends to advance to a later stage of floating meadow, building up a floating organic soil (histosol) (Neiff, 1978, 1982), which supports shrubs such as *Ludwigia nervosa* (Poir.) Hara and *Rhynchanthera novemnervia* DC. (Pivari et al., 2008) and even treelets, e.g. *Cecropia pachystachya* Trécul and *Tabebuia insignis* (Miq.) Sandw., until the pond eventually dries up and the floating meadow dies, and the process resumes in a new flood cycle (Pott and Pott, 2003). Nitrophilous terrestrial plants also appear, such as *Erechtites hieracifolia* (L.) Raf. ex DC., and the weedy tanner-grass *Urochloa arrecta* (Hack. ex T. Durand & Schinz) Morrone & Zuloaga thrives on this organic substratum. Often the floating meadow is not attached, as an island, and moves around by wind, sometimes becoming stranded on the shore and decaying, recovering only if the water rises in time; it can be carried downstream and block a channel mouth or end up in the river, losing pieces due to collisions (banks, logs) or storms (1 m waves), and finally disintegrating.

2.6. Indicator species

In the Pantanal, dominance of free-floating plants (*Pistia*, *Salvinia*) indicates that the water body has dried off or the aquatic vegetation was removed by another disturbance. In the highlands, dense populations of *Echinodorus macrophyllus* (Kunth) Micheli, and *Urospatha sagittifolia* (Rudge) Schott indicate disturbed wetland, usually occurring near roads and on silted *veredas* (Pott and Pott, 2003), while *Xanthosoma striatipes* tends to increase under grazing. The submerged *Ottelia brasiliensis* Planch. increases in dammed streams.

3. Pantanal Matogrossense National Park

As a case study, some original data extracted from the unpublished report are presented about the National Park, gathered by the authors in the year 2001. So far, there is no published work on the aquatic vegetation of this Park and the adjacent Acurizal Preserve.

Seventeen sampling sites considered representative of the aquatic habitats (Table 1) were established, inspected by boat, or some on foot in the dry period, and plants were recorded at high and low waters. Plant specimens were collected, and are kept at the CGMS (UFMS) Herbarium. Plots were not measured and varied in area.

To obtain the floristic similarity among sampling sites of aquatic vegetation the Jaccard coefficient was used (Figure 1); this is recommended for presence/absence data (Krebs, 1989). In addition, cluster analysis was performed using the Unweighed Pair Group Method with Arithmetic Mean (UPGMA) (Kent and Coker, 1992).

3.1. Types of aquatic habitats

The types of aquatic habitats and vegetation sampled were river, "corixo" (anabranch, oxbow), floating meadow, lake, pond, seasonal channel ("vazante"), backswamp and incoming stream.

The Alegre and Caracará Rivers are anabranches which run in a cutoff channel from the Cuiabá River to lake Baía dos Burros and other similar large open waters. The lakes show little aquatic vegetation cover, due to waves.

3.2. Flora

The floristic survey of various habitats at 17 sampling sites in the Park showed 135 species of aquatic macrophytes, nearly half the total number for the whole Pantanal. The most numerous families were Poaceae (15), Cyperaceae (10), Fabaceae (13), Onagraceae (9), Asteraceae (5), Convolvulaceae (5) and Euphorbiaceae (5), and the best represented genera were *Ludwigia* (13), *Cyperus* (10), *Ipomoea* (6), *Panicum* (6), *Aeschynomene* (5), *Eleocharis* (5), *Utricularia* (5) and *Polygonum* (5). These families and genera are typical of the Pantanal aquatic flora (Pott and Pott, 2000).

3.3. Life forms

The life forms are all present, albeit submerged, and some rooted floating plants are not common in the Park. It is surprising that not a single species of *Nymphaea* was detected, even though it is so easy to spot, and that seven

Table 1. Types of aquatic habitats and vegetation sampled in Pantanal Matogrossense National Park and Acurizal Preserve, Pantanal wetland, Brazil.

Sites	Abbreviation	Coordinates S, W	Habitat
Acurizal Preserve	AP-1	17° 48' 31.3" and 57° 34' 34.8"	Seasonal stream
Acurizal Preserve	AP-2	17° 48.47.5"and 57° 33' 36.9"	Oxbow lake (shallow)
Baía Acurizal	BA-1	17° 49' 51.8"and 57° 34' 55.4"	Connected large oxbow
Baía Caracará	BC-1	17° 51.32" and 57° 26.86"	Delta lake
Baía Caracará	BC-2	17° 51.71" and 57° 26.23"	Delta lake
Baía dos Burros	BB-1	17° 50' 23.7" and 57° 23' 48.7"	Closed oxbow
Baía dos Burros	BB-2	17° 49' 19.6" and 57° 22.57.5"	Oxbow lake
Córrego Retiro	CR-1	17° 50' 29.8" and 57° 33' 35.4	Incoming stream
Córrego Zé Dias	CZ-1	17° 52.06" and 57° 30.09"	Bay of stream
River Cuiabá	RI-1	17° 51' 08.3" and 57° 24' 51.5"	Backswamp
Park houses	PH-1	17° 50' 45.4" and 57° 24' 12.3"	Pond
Park houses	PH-2	17° 50' 44.7" and 57° 24' 12.4"	Backswamp
River Alegre	AL-1	17° 37' 46" and 57° 24' 46"	Anabranch
River Araminho	AR-1	17° 44.05" and 57° 32.48"	Old river bed
River Araminho	AR-2	17° 43.65" and 57° 32.37"	Backswamp
River Caracará	RC-1	17° 43.22" and 57° 20.59"	Anabranch
River Caracará	RC-2	17° 43.97" and 57° 19.81"	Anabranch

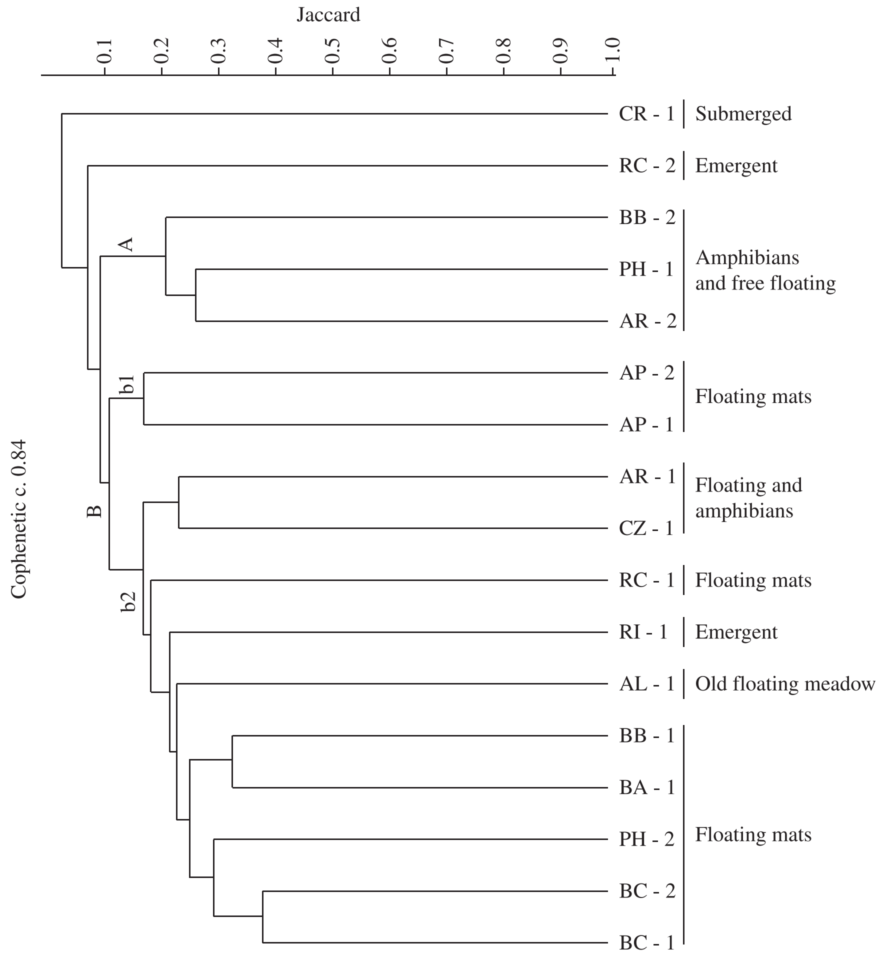

Figure 1. Dendrogram of floristic similarity among sampling sites of aquatic vegetation, grouped (separate vertical line on the right) according to their main habits, of Pantanal Matogrossense National Park and Acurizal Preserve, Pantanal wetland, Brazil. See Table 1 for names of sampling sites, coordinates and types of habitat.

species are found elsewhere in the Pantanal. Their absence is attributed to the low transparency of the water not allowing the young leaves to rise to the surface, although their relative *Victoria* succeeds in this. The turbid water would also explain the low number (five) of submerged species, four of them exclusive to the clear stream (CR-1) coming from the hill.

3.4. Main aquatic communities

Along rivers and streams there is a clear zoning of vegetation, seasonally dynamic: rooted floating mat (*Eichhornia azurea*, *Paspalum repens* Berg., *Panicum elephantipes* Nees) near the bank, then a sequence of emergent plants along the riverside, such as *Panicum dichotomiflorum* Michx. and *Paspalum fasciculatum* Willd. on the levee, oxbows and backswamps with free floating and emergent macrophytes, floating mats and floating meadows, and swamp of *Aspilia latissima* Malme. Thickets of this 1-2 m shrub, often mixed with *Polygonum acuminatum* Kunth, *Ipomoea carnea* Jacq. var. *fistulosa* (Mart. ex Choisy) D.A. Austin, and *Cissus spinosa* Cambess. are an intermediate stage between the aquatic vegetation and early successional phases of riparian forest, held back by flood and eventual wildfires. Well developed floating meadows occur on both sides of the anabranch Alegre River (AL-1), with treelets of *Tabebuia insignis* (Miq.) Sandw.), invaded by tanner-grass *U. arrecta*, while large emergent plants dominate in the anabranch Caracará River (RC-2) until further upstream becoming blocked by floating meadows. A typical oxbow lake (BB-1) is one connected to the Baía dos Burros lake, with free-floating plants and dead matter being colonised by the epiphytic *Oxycaryum cubense* plus dense mats of this sedge. Araminho River (AR) is an active old river bed, connected to the Paraguay River and anastomosed with its own oxbows.

3.5. Species richness

Species richness (Table 2) increases in wave-protected smaller water bodies and the older floating islands hold the highest number of species. On the floating meadow of the backswamp near the Park houses (PH-2) 45 species were found, nearly as many as on a floating meadow of

Table 2. Species richness, exclusive and common species at sampling sites of aquatic vegetation of the Pantanal Matogrossense National Park and Acurizal Preserve, Pantanal wetland, Brazil (meaning of site names with coordinates is given in Table 1). Common: present in ≥ 7 habitats.

Sites	Richness	Species	
		Exclusive	Common
PH-2	45	3	14
AL-1	42	10	12
BC-2	40	0	15
BC-1	34	1	13
AR-2	34	9	7
CZ-1	27	4	11
BA-1	25	1	13
RI-1	23	1	9
AR-1	22	1	8
BB-1	21	0	11
PH-1	21	2	5
RC-1	19	0	7
C-2	13	1	2
BB-2	13	0	5
AP-1	12	2	5
AP-2	11	1	5

the anabranch Alegre River (AL-1) with 42, each with one third of the aquatic floristic richness. The lowest richness was found in two sites (AP-1 and 2) on floating mats of the Paraguay River, at Acurizal Preserve, with 12 and 11 species, respectively.

3.6. Floristic similarity

Floristic similarity among sampled sites is shown in Figure 1. Cophenetic correlation explains 84% of the data. Two groups are shown in the dendrogram, A and B, with low similarity (15%). Group A joined sites AR-2, BB-2 and PH-1, which are the *Aspilia latissima* backswamps, with 25% similarity for the first two and 30% for the third site. Two other sites stand out, CR-1 and RC-2, with low similarity, below 10%; CR-1 is Córrego Retiro creek, with crystalline water from the hills, showing submerged species (*Utricularia breviscapa* Wright ex Griseb., *U. hydrocarpa* Vahl, and *Egeria najas* Planch.) and *Ludwigia sedoides* (Bonpl.) Hara, absent in the other sampled sites, whereas RC-2 is an extensive bank of large emergent plants (*A. latissima*, *I. carnea*, *Polygonum* spp.). Group B was divided in two subgroups, *b1* which linked AP-1 and AP-2, with 18% similarity, and *b2* which joins sites AR-1, CZ-1, RC-1, RI-1, AL-1, BB-1, BA-1, PH-2, BC-2, and BC-1, at different similarity levels (18 to 38%). Groupings tend to show a sequence from floating mats (BB-1, BA-1, PH-2, BC-1 and 2) to inland sites farther from the Paraguay River. The floating meadows stayed apart due to the advanced succession stage of AL-1 compared to RC-2, though both are on anabranches.

3.7. Frequency and cover

Cover was visually estimated (in 1 m^2 quadrats) for the main species per sampling site. The most frequent species and also showing the highest cover is *Polygonum acuminatum*, followed by *Eichhornia crassipes* with the second highest frequency, while *E. azurea* is the second in cover; the fourth in cover is *Oxycaryum cubense* (Table 3). So, only four species add to nearly half (46.7%) of the overall cover of the sampled aquatic vegetation. Next in frequency are *Vigna lasiocarpa*, *Hymenachne amplexicaulis*, *Mimosa pigra*, *Oxycaryum cubense*, *Aspilia latissima*, *Salvinia auriculata* and *Paspalum repens*.

Even though *Victoria amazonica* is impressive in the landscape, it is not frequent in the study area and its population (Araminho River) was seen only during the flood period. This giant water-lily is very competitive and tends to dominate other plants, expanding its 1-2 m diameter leaves with their strong symmetric frame of ironwork-like nerves, until a single individual can cover up to 20 m^2. Associated species such as *E. azurea* and *Paspalum repens* recolonise available space during the low water season.

Near the inselberg Morro do Caracará the large populations of native rice *Oryza latifolia* Desv. and *O. glumaepatula* Steud. represent important germplasm, so the Park has a role in *in situ* conservation. At low water, the flood-grown culms lie down, and are then often taken over by *Hymenachne amplexicalis* and *Leersia hexandra*, until their regrowth from nodes when the flood returns.

Lake Gaíva does not present macrophytes, only algae, indicated by the green colour of the water and the organic sediment, and by filaments on the shore.

4. Use and Conservation

Domestic animals, particularly horses, feed on aquatic plants, mainly grasses and sedges (Pott and Pott, 2004; Alho, 2008a,b). However, cows are usually removed from deep flooded areas or they spontaneously move to less flooded ground. Nevertheless, cattle remain year-round in rain-flooded zones, where they overgraze and trample waterlogged short soft grasslands around ponds and drainage lines. Buffaloes are known for damaging aquatic habitats. For instance, Pott et al. (1999) found 18 aquatic plant species in a pond with buffaloes, while 2 years after the removal of the animals the richness increased to 38 species. Fortunately buffalo are not liked by traditional ranchers, as they are difficult to manage and tend to become feral in this extensive type of husbandry, otherwise aquatic vegetation could be severely damaged, as has occurred in the Amapá wetlands in Amazonia. However, new owners have started to introduce buffalo again, as well as goats, both of which present a threat to the Pantanal.

Wildfire reaching dry beds is deleterious to hydrophytes with exposed buds, while it enhances seed germination of

Table 3. Frequency and mean cover of the main aquatic macrophytes of Pantanal Matogrossense National Park and Acurizal Preserve, Pantanal wetland, Brazil.

Species	Frequency (%)	Mean cover (%)
Aspilia latissima Malme	58.82	3.53
Urochloa arrecta (Hack. ex T. Durand & Schinz) Morrone & Zuloaga	29.41	3.53
Cayaponia podantha Cogn.	29.41	1.12
Discolobium pulchellum Benth.	41.18	0.41
Echinochloa polystachya (Kunth) Hitchc.	29.41	0.18
Eichhornia azurea (Sw.) Kunth	**58.82**	**11.24**
Eichhornia crassipes (Mart.) Solms	**64.71**	**12.24**
Eleocharis minima Kunth	17.65	4.62
Hydrocotyle ranunculoides L.f.	29.41	-
Hymenachne amplexicaulis (Rudge) Nees	47.06	0.65
Ipomoea carnea v. *fistulosa* (Mart. ex Choisy) Austin	35.29	3.70
Leersia hexandra Sw.	41.18	2.59
Lemna aequinoctialis Welw.	29.41	-
Lippia alba (Mill.) N.E. Br.	35.29	0.76
Ludwigia helminthorrhiza (Mart.) Hara	41.18	-
Ludwigia leptocarpa (Nutt.) Hara	29.41	1.12
Ludwigia nervosa (Poir.) Hara	35.29	-
Melochia arenosa Benth.	41.18	2.47
Mimosa pigra L.	47.06	1.24
Oxycaryum cubense (Poepp.& Kunth)Lye	47.06	**9.06**
Panicum elephantipes Nees	41.18	2.24
Paspalum repens Berg.	47.06	3.59
Pfaffia glomerata (Spreng.) Pedersen	29.41	0.41
Pistia stratiotes L.	29.41	-
Polygonum acuminatum Kunth	**76.47**	**14.18**
Polygonum ferrugineum Wedd.	35.29	3.88
Pontederia parviflora Alex.	41.18	-
Rhabdadenia madida Miers	35.29	0.24
Salvinia auriculata Aubl.	47.06	1.94
Vigna lasiocarpa (Benth.) Verdc.	**58.82**	-

weedy *Mimosa* spp. and *Sesbania virgata* (Cav.) Pers., shrubs which tolerate flooding and compete with other aquatic plants (Pott and Pott, 2003). Yet rhizomatous macrophytes such as *Canna glauca* L., *Cyperus giganteus* Vahl, *Eleocharis* spp., *Thalia geniculata* and *Typha domingensis* can survive and tend to become dominant (*op. cit.*).

Few exotic aquatic plants have invaded the Pantanal. One is *Sphenoclea zeylanica* Gaertn. (Sphenocleaceae, formely Campanulaceae), but it is restricted to the Paraguay River floodplain (Pott and Pott, 2000), even in undisturbed sites such as the National Park. Two introduced grasses have become weeds, torpedo-grass *Panicum repens* L. is spreading in sandy areas and tanner-grass *Urochloa arrecta* on clay (Pott and Pott, 2003). The latter is a real threat to aquatic vegetation diversity, propagated by seed, stolon, rhizome, or any fragment, carried by flood flow, taking over other aquatic plants, as is already happening in the Pantanal National Park, where we observed that the vigorous stoloniferous *Panicum elephantipes* is one of the only native grasses to match the competition.

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Plant diversity of the Pantanal wetland

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Abstract

This is a review of current studies in diversity of the flora and main vegetation types in the Brazilian Pantanal. The flora of this wetland, nearly 2,000 species, constitutes a pool of elements of wide distribution and from more or less adjacent phytogeographic provinces, such as *Cerrado*, dry seasonal forests, Chaco, Amazonia and Atlantic Forest. The most numerous group includes wide-distribution species, mainly herbs, while the second contingent comes from the *Cerrado*. Endemic plants are rare, numbering only seven. The vegetation of the sedimentary floodplain is a mosaic of aquatics, floodable grasslands, riparian forests, savannas (*cerrados*), *cerrado* woodlands, dry forests, and a large area of mono-dominant savannas, and pioneer woodlands. The main vegetation types are briefly described with their characteristic species, and their estimated areas are given according to the latest mapping.

Keywords: Cerrado, Chaco, flora, forest, savanna.

Diversidade de plantas do Pantanal

Resumo

Esta é uma revisão sobre o estado do conhecimento sobre a flora e os principais tipos de vegetação do Pantanal brasileiro. A flora da planície inundável, de aproximadamente 2.000 espécies, é um encontro de elementos de ampla distribuição e de províncias fitogeográficas mais ou menos vizinhas, tais como o Cerrado, florestas estacionais, Chaco, Amazônia e Mata Atlântica. O grupo mais numeroso é de espécies de ampla distribuição, enquanto o segundo contingente vem do Cerrado. Plantas endêmicas são raras, somente sete. A vegetação da planície sedimentar é um mosaico de aquáticas, campos inundáveis, florestas ripárias, savanas (cerrados), cerradão, floresta decidual, e uma grande parte de savanas e florestas pioneiras monodominantes. Os principais tipos de vegetação são brevemente descritos em termos de espécies características, e suas áreas estimadas são dadas conforme o recente mapeamento.

Palavras-chave: Cerrado, Chaco, flora, floresta, savana.

1. Introduction

The history of the botany of the Pantanal goes back to early European naturalists who visited the region, as reported by Sampaio (1916). Later on, Hoehne (1923), collecting beyond the confined areas along river routes, gave the first broader report on the vegetation and plant species of the old State of Mato Grosso, including the Pantanal. A few geographers gave some landscape descriptions, with scanty reports of the vegetation. Veloso (1947, 1972) and Prance and Schaller (1982) gave some details on vegetation types. With aerial photographs and the onset of satellite imaging, a general view of the physiography was shown and the first vegetation maps were produced (Furtado et al., 1982; Loureiro et al., 1982; Abdon et al., 1998). The Brazilian botanist who most collected in Mato Grosso and Mato Grosso do Sul was Hatschbach (Museu Botânico Municipal, Cutitiba), as can be verified in Dubs (1988). Quite recently local botanists and collaborators have started to collect and to publish information on the flora (*e.g.*, Pott and Pott, 1994, 1999, 2000) and the vegetation (*e.g.*, Ratter et al., 1988; Nunes da Cunha and Junk, 2001; Damasceno-Junior et al., 2005; Nunes da Cunha et al., 2007).

A brief review will be given on the state of art concerning diversity of vegetation types and main plants in the Pantanal.

2. Results and Discussion

2.1. Flora

Considering only the Pantanal plain, 1,863 species of phanerogams were listed, legumes being the most numerous (240 spp.), followed by more than 200 grasses (Pott and Pott, 1999). The list could be updated to nearly 2,000 species (Pott and Pott, 2009). The most numerous families are Fabaceae (240), Poaceae (212), Malvaceae (98), Cyperaceae (92), Asteraceae (87), Rubiaceae (62), Myrtaceae (45), Convolvulaceae (41), and the best represented genera are *Paspalum* (35), *Cyperus* (29), *Ipomoea* (24), *Panicum* (22), *Eugenia* (20), *Ludwigia* (19), *Mimosa* (18) and *Rhynchospora* (18) (Pott and Pott, 1999), with a prominence of herbaceous species, around 1,000, due to their adaptation to floodable areas, largely occupied by amphibious and grassland habitats. Pott and Pott (2000) show 242 aquatic macrophytes, lately re-counted as 280 species. There are 10 species of palms (Pott and Pott, 1994), and two additional species of *Bactris* have been found, as yet unidentified.

2.2. Phytogeography

The central position of the Pantanal in South America has allowed the encounter among distinct phytogeographic provinces, which are Amazonia to the North, the Cerrados to the East, the Meridional Forests to the South, and the Bolivian and Paraguayan Chaco to the West, favouring a great variety of vegetation types, one of the reasons for the plural term "pantanals" (Adámoli, 1982; Alho, 2008a,b; Oliveira, 2008). Uetanabaro et al. (2007, p. 280) stated that the region lies within the "central portion of the large diagonal area of open vegetation forms of South America, which goes from the Caatinga in Northeast Brazil to the Chaco in Argentina, where areas of contact occur among Pantanal, Chaco and *Cerrado*", qualifying it "of great biogeographic importance". The Meridional Forests may be considered as the Paraná basin Forest (Spichiger et al., 2007).

Due to the floristic mix, with gallery forests, palmlands, floodable grasslands, *Tabebuia aurea* savannas, *cerrados*, *cerrado* grasslands, and flood-free ridges (paleodykes) covered with *cerrado* woodlands and forests, the vegetation used to be called "Pantanal Complex", a concept dropped by Adámoli (1982), considering "mosaic" a more proper term.

The flora receives influence from some main neighbouring phytogeographic domains (Adámoli, 1982). The main influence is the group of wide distribution, mostly herbaceous species; around 160 of them are weedy. The second contingent is the *Cerrado* (with uppercase C when referring to a biogeographic province), connected to the sandy highlands where the woody savanna called *cerrados* (lowercase c to designate the vegetation form) are the main vegetation type. A great part of the areas inside the Pantanal with *Cerrado* have soils deposited by the Taquari River. The Taquari alluvial fan covers 50,000 km^2, about 30% of the Pantanal, but only a small part of it is actually occupied by *cerradão* type woodland, while most of it is covered with grasslands and floodable vegetation, with some woody elements of *Cerrado*.

The other floristic province which influences the region is the Amazon forest, mainly on the Paraguay River floodplains. The headwaters of many affluents of this river begin near the transition with the Amazon basin and so work as corridors for some species to reach the Pantanal, especially those from floodable areas (*Igapó* or *Várzea*) such as *Nectandra amazonum* Nees, *Victoria amazonica* (Poepp.) J.C. Sowerby and *Alchornea castaneifolia* (Willd.) A. Juss., or occur in a similar wetland, the Araguaia floodplains, and Lhanos de Mochos, *e.g. Vochysia divergens* Pohl. The flooding regime of the Paraguay River has a few months lag after the rains fall on the upper watersheds, to reach the Pantanal. So, when inundation occurs the dry season has already begun in the lowland, and even without local rain the Amazon species can survive due to the floods.

The next phytogeographical influence is the Chaco, which occurs mainly in Paraguay, Bolivia and Argentina. According to Prado et al. (1992) the real Chaco areas inside the Pantanal can be found only in Porto Murtinho. Nevertheless, some Chaco species can be found in other sub-regions, and the most widespread is the palm *Copernicia alba* Morong, which forms mono-dominant types in extensive areas, mainly in the South Pantanal.

Other types of flora characterising the Pantanal are the seasonal deciduous and semideciduous forests (dry forests). Both occur on ancient levees (locally called "cordilheiras"), mainly in the São Lourenço and Taquari fans. These formations have in fact two distinct origins. The semi-deciduous forest has floristic elements present in the Brazilian Atlantic Forest, according to the official Brazilian classification (IBGE, 1992), such as *Albizia hassleri* (Chodat) Burkart. The deciduous forest contains floristic elements of the Pleistocene arch (Prado and Gibbs, 1993), found in the Chiquitania (Bolivia) and in Central Brazil in connection with the *Caatingas* of NE Brazil, contributing with species such as *Amburana cearensis* (Allemão) A.C. Sm., *Phyllostylon rhamnoides* (J. Poiss.) Taub., *Sebastiania brasiliensis* Spreng., *Seguieria aculeata* Jacq., etc. Damasceno-Junior et al. (2009) estimated about 1.5 % of the Pantanal was covered with deciduous forests. Dry forests are mainly found on the calcareous hills of Corumbá and on residual plateaus of Urucum-Amolar and Bodoquena, which are part of the Paraguay Upper Basin.

2.3. Main vegetation types

According to Silva et al. (2000), *Cerrado* occupies about 36 % of the region. There are various degrees of *Cerrado* cover: more than 70% in the sub-regions of Aquidauana, Barão de Melgaço and Paiaguás (central and Eastern part of Pantanal); between 40 and 50% in the sub-regions of Cáceres, Nhecolândia and Miranda; and 10% in the sub-region of Poconé), whereas *Cerrado* vegetation is absent in the sub-regions of Nabileque and Paraguay – with dominance of Chaco and Amazonian vegetation, respectively.

According to Prance and Schaller (1982), Pott and Pott (1994, 2000) and Silva et al. (2000), there are various vegetation types in the region, and mosaics of floodable grasslands, *cerrado* woodland (*cerradão*), *cerrado*, semideciduous forest, riparian forest, swamps and floating vegetation are particularly conspicuous, plus other physiognomies. A synthesis of vegetation types is given in Table 1.

The Savanna (*Cerrado*) predominates in 50% of the Pantanal. Flood dynamics causes rapid changes in vegetation cover and promotes great diversity in pioneer types, varying from herbaceous to woody formations. In general there is a continuum from semi-deciduous forests to dry and forested savanna (*cerradão*). The species listed for the vegetation types described below were recorded during field work on inspected remnants and are based on herbarium collection and the authors' experience.

1) Seasonal Deciduous Forest (Tropical Dry Forest), found on rich or calcareous soils, presenting a tree stratum average 20 m tall with deciduousness above 50%, with two very distinct seasons (one rainy and another dry); it can be subdivided into:

1.1) Lowland Seasonal Deciduous Forest, commonly called dry forest, or calcareous forest, with more than 60% of trees dropping their leaves; species include *Anadenanthera colubrina* (Vell.) Brenan, *Aspidosperma pyrifolium* Mart., *Myracrodruon urundeuva* Allemão, *Phyllostylon rhamnoides*, *Tabebuia impetiginosa* (Mart. ex DC.) Standl., etc;

1.2) Submontane Seasonal Deciduous Forest, amongst several species, *Acacia paniculata* Willd., *Albizia hassleri*, *Anadenanthera colubrina*, *Aspidosperma pyrifolium*, *M. urundeuva*, etc. can be cited, but some are rare on the plain, such as *Chorisia pubiflora* (A. St.-Hil.) Dawson, *Sterculia striata* A. St.-Hil. & Naudin, or were not found, *e.g.*, *Acosmium cardenasii* H.S. Irwin & Arroyo, *Coutarea hexandra* (Jacq.) K. Schum.;

2) Seasonal Semi-deciduous Forest, characterised by leaf loss in 20 to 50% of trees, average 20 m tall, reaching up to 30 m. It is subdivided into:

2.1) Alluvial Seasonal Semi-deciduous Forest, also called riparian forest, found lining rivers of the basin and often periodically flooded, with denser formations found mainly along the Paraguay River, in the sub-regions of Paraguay and Poconé, and along the São Lourenço River in Barão do Melgaço, with trees such as: *Albizia inundata* (Mart.) Barneby & J.W Grimes, *Cassia grandis* L.f., *Vitex cymosa* Bertero, etc;

2.2) Lowland Seasonal Semi-deciduous Forest, occurring on flood-free ground (ridges or ancient levees), with species such as: *Anadenanthera colubrina*, *Astronium fraxinifolium* Schott, *Attalea phalerata* Mart. ex Spreng., *Copernicia alba*, *Protium heptaphyllum* (Aubl.) Marchand, *Pterogyne nitens* Tul., *Tabebuia impetiginosa*, *T. roseo-alba* (Ridl.) Sandw., etc;

3) Savanna, regionally called *cerrado* and which is already internationally accepted, is found in areas with vegetation presenting xeromorphic features due to the dry season, usually on dystrophic soils, except for the forested type. *Cerrado* and *cerrado* woodland ("cerradão") on poor sands in the central and Eastern parts of the Pantanal show a lack of palms except for the small *Allagoptera leucocalyx* (Drude) Kuntze, many Fabaceae [*Acosmium dasycarpum* (Vog.) Yakol., *Andira cuyabensis* Benth., *Bowdichia virgilioides* Kunth, *Hymenaea stigonocarpa* (Mart.) Hayne, *Vatairea macrocarpa* (Benth.) Ducke], Myrtaceae [*Eugenia* spp., *Gomidesia palustris* (DC.) Kausel, *Myrcia* spp.], and Vochysiaceae [*Qualea* spp., *Salvertia convallariodora* A. St.-Hil., *Vochysia* spp.], *Kielmeyera rubriflora* Cambess. There are few hardwoods on poorer soils, used for fencing, usually legumes, *e.g.*, *Dipteryx alata* Vog., *Diptychandra aurantiaca* (Mart.) Tul., *Plathymenia reticulata* Benth.; also *Lafoensia pacari* A. St.-Hil. Other common *Cerrado* trees: *Aspidospermum tomentosum* Mart., *Byrsonima coccolobifolia* Kunth and *Caryocar brasiliense* Cambess.

During dry years some *cerrado* and other pioneering species "invade" grasslands, even occurring in dried-out pond beds: in sandy areas, *Annona dioica* A. St.-Hil., *Bowdichia virgilioides*, *Buchenavia tomentosa* Eichler, *Caryocar brasiliense*, *Curatella americana* L., *Hymenaea stigonocarpa*, *Luehea paniculata* Mart., *Simarouba versicolor* A. St.-Hil., etc.; on clay, other species increase, *e.g. Callisthene fasciculata* (Spreng.) Mart. and *Tabebuia aurea* (Manso) Benth. & Hook. f. ex S. Moore, etc.

3.1) Forested Savanna, called "Cerradão", is a denser woodland where tree canopies touch each other and part of the species are semi-deciduous, 8 to 15 m tall, occurring more in the East and centre of the plain, on sandy soils (sub-regions of Cáceres, Barão do Melgaço, Nhecolândia, Aquidauana and Miranda), on flood-free ground; some of the species are: *Byrsonima crassifolia* (L.) Kunth, *Caryocar brasiliense*, *Dimorphandra mollis* Benth., *Eriotheca gracilipes* (K. Schum.) Robyns, *Kielmeyera coriacea* Mart., *Qualea grandiflora* Mart., *Q. parviflora* Mart., *Xylopia aromatica* (Lam.) Mart., etc;

3.2) Woody Savanna, also called *cerrado* grassland, *cerrado* or open *cerrado*, is a form of *cerrado stricto sensu*, well represented in the Pantanal, with shrubs and scattered trees up to 10 m tall, with thick bark and tortuous trunks, on a predominant grassy/herbaceous stratum, occurring more in the Eastern and central parts of the plain, on sandy soils

Table 1. Quantification (km^2) of the vegetation cover of the Pantanal, mapping based on Landsat images of the year 2002. Vegetation names according to the official Brazilian nomenclature (IBGE, 1992), common terms in parentheses.

Phytoecological region, formation or subtype	Area (km^2)
I – Semi-deciduous Seasonal Forest	
Alluvial forest (riparian forest, gallery forest)	6,131.0
Submontane forest (dry forest)	92.3
II – Deciduous Seasonal Forest	
Alluvial forest (riparian forest, gallery forest)	9.6
Lowland forest ("Mata", dry forest, calcareous forest)	519.0
Submontane forest ("Mata", dry forest, calcareous forest)	910.0
III - Savanna (*Cerrado*)	
Forested (*Cerrado* woodland, *Cerradão*)	8,984.0
Wooded (*Cerrado* grassland, *Cerrado*, open *Cerrado*), with and without gallery forest	25,205.9
Grassy-Woody (Grassland, open grassland, bushy grassland, *Elyonurus* grassland, and flooded grassland), with and without gallery forest	8,880.7
Forested + Wooded and Wooded + Forested	80.3
Wooded + Grassy-Woody and Grassy-Woody + Wooded	734.5
IV – Steppic Savanna (Chaco)	
Wooded	213.3
Park ("Carandazal")	6,590.7
Grassy-Woody ("campo")	4,526.1
Wooded + Forested	80.3
Wooded + Grassy-Woody	244.2
Grassy-Woody + Grassy-Woody	490.3
V – Pioneer Formations: Vegetation with Fluvial and/or Lacustrine Influence: *Mauritia* palmland ("Buritizal"), Spiny scrub ("Espinheiral"), *Vochysia divergens* woodland ("Cambarazal"), Giant sedge ("Pirizal"), tussock grassland ("Macega"), *Couepia uiti* woods ("Pateiral"), *Licania parvifolia* woods ("Pimenteiral"), Fireflag ("Caetezal"), Swamp, floating meadow and bushy grassland	5,216.2
VI – Areas of ecological tension or floristic contacts	
Ecotone	
Savanna/Deciduous Seasonal Forest ("Mata")	315.9
Savanna/Semi-deciduous Seasonal Forest ("Mata")	2,258.5
Deciduous Seasonal Forest/Pioneer Formations ("Mata")	4,697.4
Savanna/Pioneer Formations (*Cerrado*, Bushy Grassland, "Cambarazal")	16,429.5
Steppic Savanna/Deciduous Seasonal Forest ("Mata")	803.9
Enclave	
Savanna/Deciduous Seasonal Forest ("Mata")	904.9
Savanna/Deciduous Seasonal Forest ("Mata")	53.3
Savanna/ Semi-deciduous Seasonal Forest ("Mata")	298.5
VII – Vegetation refuges (remnant communities): Herbaceous submontane refuge (Grassland)	28.4
VIII – Anthropic areas	
Secondary vegetation (of Savanna, Forest, Forested and Park Steppic Savanna)	403.6
Agriculture	411.5
Sown pasture (in Seasonal Forest, Savanna and Steppic Savanna)	16,511.8
IX – Other Anthropic Areas: Urban Influence + Mining degraded areas	132.7
X – Others: Water bodies (rivers, streams, oxbows, channels, lakes, ponds, brackish ponds)	2,557.3
TOTAL	151,186.2

Source: Silva et al. (2007).

(sub-regions of Cáceres, Barão do Melgaço, Paiaguás, Nhecolância, Aquidauana and Miranda), on lower areas, tending to grassland as the degree of inundation increases, or the opposite, to woodier when drier. The most common species found are: *Annona dioica*, *Buchenavia tomentosa*, *Curatella americana*, *Dimorphandra mollis*, *Luehea paniculata*, *Qualea parviflora*, *Simarouba versicolor* and *Stryphnodendron obovatum* Benth., among others;

3.3) Park Savanna (Park of *Cerrado*) occurs in floodable areas, normally with dominance of a single tree or shrub species over a grassy stratum:

3.3.1) *Byrsonima orbignyana* scrub ("canjiqueiral") – homogeneous shrubby formation, 1-5 m tall, dominated by *B. orbignyana* A. Juss., on sandy or silty soils, floodable (*ca.* 50 cm deep), in the sub-regions of Paiaguás, Nhecolândia, Aquidauana, Abobral and Cáceres; as a pioneer woody element, it is considered a pasture weed, and in past decades it was the main controlled species. *Byrsonima orbignyana* savanna, on floodable sandy areas, also sometimes occurs on ancient silted drainage channels amongst *Tabebuia aurea* savanna and spread over most of the plain;

3.3.2) *Curatella americana* ("lixeiral") – a sort of park savanna dominated by this tree, which occurs in floodable areas; often it is associated with slightly higher ground, while it is a rather shrubby (multi-stem) dwarfed shrub on ill-drained land or a *ca.* 15 m tall tree in flood-free woodland (Pott and Pott, 2004, 2005); it is the most frequent woody species in the Pantanal, being very abundant on the dystrophic sands of the Eastern zone (Pott and Pott, 2004), and in the earth-mound savanna in the Northern part of the floodplain (Ponce and Nunes da Cunha, 1993); it is also considered a weed by ranchers, mainly during dry years (Pott and Pott, 2004);

3.3.3) *Tabebuia aurea* ("paratudal") – floodable savanna with a single tree species stratum, mean density of 363 individuals/ha (Soares and Oliveira, 2009), 5-12 m tall, generally growing on a type of earth-mound or termite-like hummocks; other woody species (*e.g. Astronium fraxinifolium*) appear in drier years, but are kept back by wildfires or return of floods; occurs mainly in the South of the Pantanal between the rivers Nabileque and Miranda, associated with slightly alkaline waters and sediments (Pott, 1994); it used to be interpreted as *cerrado* (Furtado et al., 1982; Loureiro et al., 1982), but lately it has been considered to be linked to the Chaco flora (Silva et al., 2007), due to the associated species, such as *Aposorella chacoensis* (Morong) Spegazz., *Camptosema paraguariense* Chodat & Hassl., *Dolichopsis paraguariensis* (Benth.) Hassl., *Prosopis rubriflora* Hassl., etc. (Pott, 1994), and because such vertic soils do not exist under *Cerrado*.

3.4) Grassy-woody Savanna, called *Campo* or flooded grassland, normally made up of grasses and herbs. It can be divided into flooded and dry grasslands, the proportions varying in function of local rainfall and/or river overflow, representing 31.1% of the vegetation of the region, being more associated with drainage factor than soil fertility. Higher predominance in some portions of the Pantanal (Abobral, Paiaguás, Nhecolândia and Nabileque), with dominance of grasses and sedges. Among coarse grasses [*Andropogon* spp., *Paspalum carinatum* Humb. & Bonpl., *P. lineare* Trin. and *Trachypogon spicatus* (L. f.) O. Kuntze], there are other species such as wild-rice *Oryza* spp., *Mesosetum* spp., *Reimarochloa* spp., *Paratheria prostrata* Griseb., plus *Paspalum* spp., *Digitaria* spp., *Panicum* spp. Some species are found more on poor soils, such as *Axonopus purpusii* (Mez) Chase, while *Paspalum almum* Chase is associated with fertile soils. Grasslands, depending on cycle of flood or drought, can be taken over by woody vegetation of *cerrado*, or vice-versa.

4) Steppic Savanna, commonly called Chaco and linked to the floristic province of Chaco in Argentina, Paraguay and Bolivia; the only true Brazilian Chaco occurs at the SW end of Mato Grosso do Sul and belongs to the *Chaco Húmedo* (Prado et al., 1992). There is a predominance of spiny vegetation with features of semi-arid vegetation (presence of xeromorphic species, plus cacti), with physiognomy similar to the Brazilian *Caatinga*, although it also contains wet areas, mainly in the Eastern Chaco; it is present on salty clays in the sub-regions of Nabileque and Porto Murtinho, and can be subdivided into four vegetation forms:

4.1) Forested Steppic Savanna, commonly called Chaco, dry forest or Chaquenian forest, with dry forest appearance, deciduous, average 5-7 m tall; some typical species are *Aspidosperma quebracho-blanco* Schltdl., *Caesalpinia paraguariensis* (D. Parodi) Burkart, *Diplokeleba floribunda* N.E. Br., *Parkinsonia praecox* (Ruiz & Pav. ex Hook.) J. Hawkins, *Piptadenia viridiflora* (Kunth) Benth., *Prosopis rubriflora*, *P. ruscifolia* Griseb., *Schinopsis balansae* Engl., *Zizyphus oblongifolius* S. Moore, etc.; lately undergoing strong deforestation;

4.2) Steppic Scrub Savanna, also called Chaco, is similar to the previous one, but with shorter and spaced trees, interspersed in a stratum of spiny treelets which normally do not surpass 4 m, such as *Acacia farnesiana* Willd., *A. paniculata*, *Capparis retusa* Griseb., *C. speciosa* Griseb., *C. tweediana* Eichl., *Celtis pubescens* Kunth, *Zizyphus* spp., etc., and frequently a ground cover of *Selaginella sellowii* Hieron.;

4.3) Steppic Park Savanna ("Carandazal", "Campina de Carandá") – made up of a grassy sward and a woody stratum with predominance of the palm *Copernicia alba*, 8-20 m tall, occurring mainly in the Southern Pantanal, in large areas of the sub-regions Nabileque and Porto Murtinho, on black alkaline or saline clays, with sub-surface calcium carbonate concretions; it also occurs on sandy soils, if fertile or high pH, as around brackish ponds (Nhecolândia) or shell-derived hummocks (Abobral), in floodable areas, while on drier patches it becomes denser, as palm woodland, with associated species such as *Capparis speciosa*, *Cereus bicolor* Rizzini & Mattos, *Diplokeleba floribunda*, *Machaerium hirtum* (Vell.) Stellf., *Mimosa* spp., *Prosopis ruscifolia*, *Tabebuia nodosa* (Griseb.) Griseb., etc;

4.4) Steppic Woody-grassy Savanna, various types of grassland, such as open grassland, bushy grassland, flooded grassland or spiny grassland, made up of a grassy sward with spiny dwarf plants; common species: *Acacia farnesiana*, *Celtis spinosa* Spreng., *C. pubescens*, *Mimosa* spp., *Paspalum simplex* Morong, etc;

5) Pioneer formations or monodominant vegetation types – areas under fluvial and/or lacustrine influence (sedimentation habitats, periodically or permanently flooded), made up of unstable ground covered by vegetation in constant succession, such as *Vochysia divergens*, spiny scrub, giant sedge stands, plus others described below. This type of vegetation, a result of abiotic (soil and/or hydrological) factors, allows the presence of various types of association, few plant species dominating large areas, forming typical landscapes with their local names in brackets:

5.1) *Attalea phalerata* ("acurizal") – homogeneous or mixed forest understory made up of this shady palm, occurring on flood-free ridges and grooves and on river banks, which are periodically flooded by flowing water; it often indicates anthropic action, as it can colonise cleared or frequently burned areas;

5.2) *Attalea speciosa* palmland ("babaçual") – homogeneous dense forest predominantly of this palm, 10-22 m tall, occurring in the extreme North of Cáceres sub-region and central Nhecolândia (0.3% of the region); some dry forest trees grow inside, held back by periodical fires, such as *Astronium fraxinifolium*;

5.3) Floating mats ("camalote") and floating islands ("baceiro", "batume") – both found in permanent water bodies such as ponds, lakes, canals, oxbows and rivers; floating mats are attached banks of floating macrophytes, or not anchored, which then float downriver or move by wind; the main species are the water hyacinths *Eichhornia crassipes* (Mart.) Solms and *E. azurea* (Sw.) Kunth, both rooted or free-floating, and other aquatic plants, water lettuce *Pistia stratiotes* L. and water fern *Salvinia auriculata* Aubl., free-floating; floating meadows have denser vegetation, made up of grasses and sedges, mainly *Oxycaryum cubense* (Poepp. & Kunth) Lye and *Eleocharis plicarhachis* (Griseb.) Svens., rooted on histosol (decomposing organic material) (Pivari et al., 2008) accumulated on the densely entangled roots, most frequent in the sub-regions of Abobral and Cáceres and along the rivers Paraguay, Cuiabá, Negro, Miranda and Nabileque;

5.4) Swamp ("brejo") – permanently flooded or waterlogged areas, except in drier years, are confined to a few places, such as the Negro River (Aquidauana) and sub-regions of Abobral, Paraguay and Poconé; contains shrubby species, climbers, grasses and sedges, often forming dense thickets of spiny shrubs (*Byttneria filipes* Mart. ex K. Schum., *Mimosa weddelliana* Benth., etc.) and vines (*Cissus spinosa* Cambess., *Combretum* spp., *Ipomoea* spp.). Giant sedge *Cyperus giganteus* Vahl ("pirizal") and fireflag *Thalia geniculata* L. ("caetezal") is a sort of swamp or temporary pond dominated by these herbaceous species, mainly in the sub-regions of Abobral, Nabileque and Poconé, and increasing in the flooded Taquari delta; cat-tail *Typha domingensis* Pers. ("taboal") is a similar tall aquatic herb which occurs in permanent or temporary ponds and increases in disturbed flooded areas;

5.5) *Vochysia divergens* woodland ("cambarazal") – homogeneous formation of an Amazonian tree, 5-18 m tall, on clay or loamy soils, tolerates periodical flood well, but not permanently; found mainly in the sub-regions of Barão do Melgaço, Poconé and Paraguay, adding up to 3.2% of the Pantanal vegetation, in fact much more nowadays; it is a pioneer which forms dense pure stands, considered a natural grassland weed for shading out grasslands (Allem and Valls, 1987). Since 1980, large areas have been invaded on floodplains of the Cuiabá and Paraguay rivers, now also on the lower Taquari flooded delta (Pott and Pott, 2005), but it slowly dies back under permanent deep flood;

5.6) *Elyonurus muticus* grassland ("caronal"), on intermediate, and only occasionally flooded or flood-free sandy ground, lately being replaced to cultivate *Brachiaria humidicola* Rendle or other exotic grasses;

5.7) *Bromelia balansae* stands ("gravateiro") – community of a pineapple-like plant, generally indicating flood limit; when in large amounts inside groves and woods, it may indicate selective logging with opening of gaps, which allow fast growth and spread, blocking passage of large animals, then the leaves have very spiny edges; it is not viable to map it yet;

5.8) *Couepia uiti* scrub ("pateiral") – native grassland area invaded by this tree species, considered a weed (pioneer), being abundant on sandy soils on floodplain and among riparian vegetation;

5.9) *Licania parvifolia* scrub ("pimenteiral") – native grassland areas invaded by this pioneer tree, occurring over nearly the whole Pantanal floodplain;

5.10) *Tabebuia heptaphylla* woods ("piuval"), a deciduous tree occurring in savanna or woodland, in floodable areas, generally not far from rivers and seasonal streams, tending to riparian forest in the succession;

5.11) *Mauritia flexuosa* palmland ("buritizal") – almost homogeneous formation of "buriti" palm, 5-15 m tall, with restricted distribution near the Eastern border of the plain, along the Aquidauana and Taquari Rivers, and in Barão de Melgaço;

5.12) *Erythrina fusca* woods ("abobral") – one of the main trees, usually in groups, along the Paraguay River in the Cáceres sub-region, also spread along the margins of the Aquidauana river; the flowers are visited by psittacids;

5.13) *Xylopia aromatica* savanna ("pindaival") – *Cerrado* tall shrub or tree community common in the NE of the plain.

2.4. Remarks upon vegetation types

- Dry forests – Dry forests, more abundant on the hills rather than on the plain (Hoehne, 1923; Prance and Schaller, 1982; Ratter et al., 1988), were recently described in more detail by Damasceno-Junior et al. (2009). This vegetation type covers *c.* 4% of the Pantanal, as few significant areas occur on the plain: Mata do Cedro and Fuzil in Paiaguás, Mata do Bebe in Barão de Melgaço, and other scattered patches in South Poconé, Abobral, Miranda, around brackish ponds in SE Nhecolândia, Soldado and Porto Murtinho (Damasceno-Junior et al., 2009). Typical species are: *Acrocomia aculeata* (Jacq.) Lodd. Ex Mart., *Astronium fraxinifolium*, *Casearia gossypiosperma* Briq., *Combretum leprosum* Mart., *Cordia glabrata* (Mart.) A. DC., *Dipteryx alata*, *Myracrodruon urundeuva*, *Pisonia zapallo* Griseb., *Pouteria gardneri* (Mart. & Miq.) Baehni, *Pterogyne nitens*, *Rhamnidium elaeocarpum* Reiss., *Spondias mombin* L., *Sterculia apetala* Karst., *Tabebuia impetiginosa*, *Zanthoxylum caribaeum* Lam., etc. (Damasceno-Junior et al., 2009). The Chaco influence becomes stronger southwards, as in the areas of Soldado and Porto Murtinho. Some of the dry forest areas can be interpreted as a junction of many ancient levees, generally an alluvial fan built at the earlier encounter of a tributary with the calm flood waters of a larger river. For example, sediments of the Taquari River were deposited where they met the still flood waters of the Paraguay River, before the Paraguay was gradually pushed westwards.
- Riparian forests – Most information on gallery forests is given by Damasceno-Junior et al. (2005), for the Southern part of the Pantanal, and by Nunes da Cunha and Junk (2001), for the Northern sub-regions. Some riparian trees are sort of generalists, found along almost every water course, such as *Andira inermis* Kunth and *Inga vera* ssp. *affinis* (DC.) T.D. Penn., whereas others tend to be more frequent on heavily flooded clay, *e.g.*, *Albizia inundata* and *Sapium obovatum* Klotzsch ex Müll. Arg. In the Northern section of the Paraguay River on the plain a few grow in nearly pure stands, such as *Erythrina fusca* Lourt. and *S. obovatum*, often like orchards, and some Amazonian species occur which have not been found much downstream, such as *Brosimum lactescens* (S. Moore) Berg and *Sloanea garckeana* K. Schum., plus an as yet unidentified red-fruited species of *Bactris*. Along some outgoing temporary streams (diffluents) of the Taquari River, there occur dense stands of *Tapirira guianensis* Aubl., hardly seen elsewhere in the Pantanal. It seems rather paradoxical that some trees share very distinct habitats, such as the riverside and dry forests; for example, *Albizia hassleri* and *Vitex cymosa*. Many species of gallery forests of upland streams do not grow on the plain, or only as far as the river is fast-flowing, such as *Hirtella gracilipes* (Hook. F.) Prance and *Licania humilis* Cham. & Schltdl. on the Taquari River, still close to the Eastern border. A curious case is *Salix humboldtiana* Willd., which has restricted occurrence on sandy levees of the Aquidauana River at the very entrance to the plain; after a disjunction it reappears on heavy clay along the Paraguay River at the far end of the Pantanal. Below Corumbá the Paraguay River does not often exhibit a proper riparian forest, but pioneer stages of flexible shrubs, which withstand flood flow, such as *Alchornea castaneifolia*.

Due to the dynamics of the rivers, strips of "old" forest are eroded away and new ones start on the opposite bank, where sediments accumulate and become first colonised by aquatic plants, often nearly mono-dominant, mainly grasses (*Panicum dichotomiflorum* Michx., *P. pernambucense* (Spreng.) Mez ex Pilg., *Paspalum fasciculatum* Willd.) and sedges (*Cyperus*, *Fuirena*, *Rhynchospora*), *Polygonum* spp., then subshrubs [*Aspilia latissima* Malme, *Ipomoea carnea* var. *fistulosa* (Mart. ex Choisy) D.F. Austin], shrubs (*Alchornea castaneifolia*), later trees, all entangled with a great mass of vines, such as *Combretum lanceolatum* Pohl, *Cissus spinosa*, *Mikania* spp. Some of the main species of riparian forests are: a) early stage of succession with *Cecropia pachystachya* Trécul, *Ruprechtia brachysepala* Meisn., *Inga vera*, *Sapium obovatum* and *Vochysia divergens*; b) late successional stage trees are, for example *Erythrina fusca*, *Ficus* spp., *Genipa americana* L., *Pouteria glomerata* (Miq.) Radlk. and *Triplaris americana* L. Succession stages frequently occur in progressive chronological zoning, but are also intermingled due to gaps caused by flood or fire. Along seasonal streams often grows a hedgerow of *Licania parvifolia* Hub., sometimes *Calophyllum brasiliense* Cambess. The sequence described here depends on the level of inundation that the considered river can reach, and on the region drained.

Riparian species may grow many kilometres from the river, such as *Combretum lanceolatum*, *Licania parvifolia* and *Vochysia divergens*, often in closed mono-dominant populations, therefore frequently considered undesirable invasive woody plants, as they may take over and even shade out useful grasslands.

- Grasslands – Allem and Valls (1987) produced the first comprehensive study, a benchmark on natural grasslands of the Pantanal. Grasslands are by far the biggest vegetation type of the Pantanal. Often the open landscape is mistaken for deforested area, instead of natural vegetation due to seasonal flood, even though there is some spotty shrub control done by ranchers. The effect of flood holding back woody vegetation can be observed during years without flood, when grasslands become shrubby, as during the last 15 years.

Grassland composition depends so much on flood level that a few centimetres difference is enough to determine change in species. Besides the main grasses, there is a great number of herbaceous plants, annuals or perennials, most of them growing in particular conditions of flood or soil, and these may be indicators, for example: therophytes or annual species propagated by seed (*Bacopa arenaria* (J.A. Smith) Edwall, *Heliotropium filiforme* Lehm., *Ludwigia octovalvis* (Jacq.) Raven, *Sacciolepis myuros* (Lam.) Chase); indicators of clay [annuals *Brachiaria adspersa* (Trin.) Parodi, *Eriochloa punctata* (L.) Desv., *Heliotropium procumbens* Mill., and perennials *Hemarthria altissima* (Poir.) Stapf & Hubb., *Paspalum millegrana* Schrad.]; indicators of salinity [annuals *Microchloa indica* (L.f.) Beauv., *Sporobolus pyramidatus* (Lam.) Hitchc., *Tripogon spicatus* (Nees) Ekm., and perennial *Paspalum vaginatum* Sw.]; and indicators of poor soils [*Gymnopogon spicatus* (Spreng.) O.Kuntze, *Leptocoryphium lanatum* (H.B.K.) Nees, *Mesosetum cayennense* Steud., *Panicum stenodes* Griseb.] (Pott, 1988).

2.5. Endemic and rare species

As the Pantanal is a geologically-recent (Holocene) Quaternary floodplain, very few endemic species have been found, such as *Arachis diogoi* Hoehne, *A. hoehnei* Krapov. & W.C. Greg., or new and also endemic plant species, *e.g.* *Arachis vallsii* Krapov. & W.C. Greg., *Euplocca pottii* J.I.M. Melo, *Habranthus pantanensis* Ravenna, *Stilpnopappus pantanalensis* H. Rob., *Xanthosoma pottii* E.G. Gonçalves. Some are endemics in the broad sense, such as *Bergeronia sericea* Mich. and *Lonchocarpus nudiflorens* Burkart. There seem to be more endemic plants on surrounding hills than on the plain, such as *Aspilia grazielae* Santos, *Discocactus ferricola* Buining & Bradero, *Gomphrena centrota* Holzh., *G. matogrossensis* Suessenguth, *Lonchocarpus variabilis* R.R. Rodrigues & Tozzi, *Mentzelia corumbaensis* Hoehne, *Mimosa ferricola* R.R. Silva & A.M.G.A. Tozzi, *Deuterocohnia meziana* Kuntze ex Mez, etc.

- Rare species: *Cereus saddianus* Rizz. & Mattos, *Dieffenbachia aglaonematifolia* Engl., *Discolobium psoralifolium* Benth., *Eichhornia diversifolia* (Vahl) Urb., *Evolvulus pterygophyllus* Mart., *Eulophia alta* (L.) Fawc. & Rendl., *Habenaria nabucoi* Ruschi, *Ipomoea piresii* O'Donell, *Ludwigia affinis* (DC.) Hara, *Nymphaea belophylla* Trickett, *Utricularia trichophylla* Spruce ex Oliv., *Xanthosoma aristiguietae* (Bunting) M. Madison.

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The floristic heterogeneity of the Pantanal and the occurrence of species with different adaptive strategies to water stress

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Abstract

The Pantanal is characterised by a diversity of environments with areas ranging from periodic or permanent heavy flooding to areas with low flood levels, and even environments that never flood. Plant species which inhabit the floodplain are distributed in specific niches, with influence of various phytogeographic domains, including the Seasonal Semi-deciduous Forest, Amazon Rainforest, *Cerrado* and *Chaco*, as well rocky remnants, with a wide ecological span in their components. In intensely flooded areas, aquatic macrophytes are widely distributed, with their dynamics closely linked to time, depth and extent of flooding. Although the term "Pantanal" suggests a huge swamp-type wetland, water level variation during a seasonal cycle does not directly reach the root system of many plants. The landscape diversity of the Pantanal wetland is molded by the flood pulse, which interferes with the dynamics of plant communities. Therefore, the retraction and expansion of populations or communities is reflected in important ecological characteristics, considering the variety of morphological, anatomical and ecophysiological features of the species, whose phenotype is the result of a particular genotype. The present study discusses peculiar issues in the adaptation of species distributed in the Pantanal biome and underscores the importance of multidisciplinary approaches to obtain conclusive data on adaptive studies.

Keywords: flood pulse, ecophysiological features, adaptation of species.

A heterogeneidade florística do Pantanal e a ocorrência de espécies com diferentes estratégias adaptativas ao estresse hídrico

Resumo

O Pantanal caracteriza-se pela diversidade de ambientes com áreas que variam desde intenso alagamento, periódico ou permanente, a áreas com baixo índice de alagamento até ambientes nunca alagados. Espécies vegetais que habitam a planície distribuem-se em nichos específicos, com influência de vários domínios fitogeográficos, entre eles a Floresta Estacional Semidecidual, Floresta Amazônica, Chaco e Cerrado, além de remanescentes rochosos, prevalecendo grande amplitude ecológica de seus componentes. Nas áreas de intenso alagamento, macrófitas aquáticas se distribuem amplamente, com dinâmica intimamente ligada ao tempo, intensidade e amplitude de alagamento. Apesar de o termo Pantanal induzir a ideia de ambiente de alagamento intenso, para muitas espécies, as variações do nível da água num ciclo sazonal não atingem o sistema radical diretamente. A diversidade de paisagens na planície é moldada pelo pulso de inundação que interfere diretamente na dinâmica das comunidades de plantas. Assim, retração ou expansão de populações ou comunidades, reflete características ecológicas importantes, a exemplo do aparato morfológico, anatômico e ecofisiológico das espécies, cujo fenótipo é resultante de genótipo particular. Neste trabalho, são discutidas questões peculiares sobre a adaptação das espécies distribuídas no bioma Pantanal e ressaltada a importância de abordagens multidisciplinares para obtenção de dados conclusivos em estudos adaptativos.

Palavras-chave: pulso de inundação, aparatos ecofisiológicos, adaptação de espécies.

1. Diversity of Environments of the Pantanal Wetlands

The Pantanal is characterised by the heterogeneity of vegetation units, which occupy distinct environments created by fluvial morphogenesis (Adámoli and Pott, 1996; Oliveira, 2007). Several plant families inhabit typical floodable fields, widely distributed in the Pantanal wetland depressions, as well as the *cordilheiras* (strands of elevated soil with unflooded woody vegetation) and *capão* (circular or elliptical forest distributed on periodically flooded natural grassland matrix) (Damasceno-Junior et al., 1999). In the Pantanal wetlands, which constitute about 35% of the Upper Paraguay River Basin (*Bacia do Alto Paraguai*) area, several minor watersheds drain large headwater areas, which are responsible for the vast flood area of the plain. Although the Pantanal is associated with the Paraguay River floodplain and its tributaries, along the wetland occur microbasins arising from the residual relief hills throughout the entire western edge of the Pantanal (Abdon and Silva, 2006).

Among the landscape units the Urucum Residual Plateau (*Planalto Residual do Urucum*) stands out, a formation which holds the *Maciço do Urucum*, a priority area for conservation, because of its composition and richness of plant species (Brasil, 1999) and endemism. It presents isolated hills located in low areas, with altitudes between 300 and 1000 m, entisols and podzol and low humic gley, covered by submontane seasonal semi-deciduous forest and lowland forests (Alho and Gonçalves, 2005). Damasceno-Junior et al. (2005) cite the rocky vegetation formations, shrubby grassland (*campo sujo*), *cerrado*, closed woodland (*cerradão*) and semi-deciduous and deciduous forests, as the phytophysiognomies of this formation.

The remnants of rock formations of limestone, sandstone, iron and manganese distributed singly or in North-South axis ridges in the wetland, currently suffer major anthropogenic pressure to extract ore. These areas hold grasslands with particular flora along an altitudinal gradient and, although the floristic inventories are still insufficient to determine the species richness, there is apparently a considerable degree of endemism, with the occurrence of *Aspilia grazielae, Gomphrena centrota* (Pott et al., 2000) and *Vernonia pottii* (Esteves, 2005) being reported on these rock formations. In the low altitude areas the endemic species *Arachis diogoi, A. vallsii, Maranta pantanensis, Stilpnopappus pantanalensis* and *Xanthosoma pottii* stand out (Pott and Pott, 2009). It is suggested that the low level of endemism found in the Pantanal is a consequence of its recent emergence (Quaternary), with insufficient time for the speciation processes (Junk et al., 2006).

Although the term "Pantanal" refers to a region with essentially hydrophyte vegetation, common in swamps, xerophytic and mesophytic species are also distributed in various landscape units, with floristic composition influenced by phytogeographic provinces of *Cerrado*, Amazon Rainforest, Semi-deciduous Forest and *Chaco* (Damasceno-Junior et al., 2005; Oliveira, 2008). The phytophysiognomies of these provinces are mixed in the Pantanal wetlands, in floodable and flood-free areas, in edge areas and on the plateaus.

Alho (2008a,b) emphasises the remarkable combination of xerophytic and mesophytic vegetation growing side by side in seasonally flooded areas in the Pantanal. Tree and shrub species occur at periodically flooded spots, or in areas not subjected to the flood pulse effect of the annual cycle. However, many herbaceous plants and aquatic macrophytes occur in areas with particular water variation or those permanently flooded. Thus, the Pantanal landscape is shaped by water regime, and its dynamics reflect the local rainfall and, mainly, changes in water level corresponding to rainfall in the headwaters of Paraguay River tributaries.

The floristic composition of a certain region is dynamic and probably continues to change over time. On a local scale, this can be exemplified by the seasonal cycle of the Pantanal, where, due to its multiannual period of flood and drought with distinct intensity and duration (Pott and Adámoli, 1996), the species succession and composition in flooded fields is peculiar, and therefore the population dynamics is markedly affected by water regime. The retraction or expansion of the populations or communities are reflected by important ecological characteristics, considering the variety of morphological, anatomical and ecophysiological features of the species, whose phenotypes are the result of a particular genotype (Fahn and Cutler, 1992).

When analysing the morphoanatomical adaptations of Pantanal plants, it is possible to classify them according to their habitats: species that inhabit regions strongly influenced by flood pulse – Pantanal sensu stricto –, and those regions which are not influenced by periodic flood – Pantanal sensu lato (which comprise all species distributed in the biome). Plant species or communities that naturally grow in a given environment share morphoanatomical characteristics and compatible physiological balances (Larcher, 2004; Fahn and Cutler, 1992), which make them adapted to that particular condition. For Fahn and Cutler (1992), adaptation results from the interrelationships of living organisms and the environment they inhabit and from the evolutionary changes throughout the life history of several classes of organisms in their particular environment.

Thus, understanding the structure of plant organs and tissues in relation to the environment for which they were selected during their evolutionary course, involves studies of ecological anatomy, and these must be conducted in a multidisciplinary way, complemented by genetic and ecophysiological studies. With these studies, it is possible to answer more precisely whether the characteristics described are merely phenotypic plasticity or if they are the reflection of genetic changes.

Extensive Pantanal floodable areas consist of monodominant formations of tree populations. Among them can be mentioned the areas of *Tabebuia aurea* (Manso) Benth.et Hook., locally known as *paratudal*, areas with *Tabebuia heptaphylla* (Vell.) Tol., known as *piuval*, the formation known as *cambarazal* comprised of

Vochysia divergens Pohl, the *lixeiral* comprised of *Curatella americana* L. and *carandazal* of *Copernicia alba* Morong (Pott, 1994). It is noteworthy that these species are also distributed in plant communities of other biomes, but it is only in the Pantanal that they form large monodominant populations of varying size and shape, reaching an area of 1,000 hectares or more. These species maintain part of the shoot and root system in the anoxic environment for periods ranging from 1 to 4 months.

The physical environmental characteristics are very distinct, when comparing the Pantanal, *Cerrado* and Semi-deciduous Forest. This makes the evaluation of species with wide distribution an interesting target for research. A recent work by Holsback-Menegucci et al. (2008) evaluated young plants of *Guazuma ulmifolia* Lam. (Malvaceae) that were artificially flooded for 100 days. These were from two populations, one from the Paraná River Basin and the other from the Pantanal. Higher growth and biomass of aerial portions were observed in the Pantanal plant population, while hypertrophied lenticels were seen in the seedlings of the Paraná River Basin population, indicating distinct ecophysiological and morphoanatomical responses in both populations.

This may indicate that populations of the same species occurring in vegetation formations with different abiotic selection pressure express distinct phenotypes in ecophysiological terms, unaccompanied by differentiation of the reproductive organ morphology, which is usually used to characterise the species. This may be merely phenotypic plasticity or may be already genetically established. Santiago and Paoli (2007) pointed out that large morphology variations in response to flood do not determine the ecophysiological tolerance of the species to it, indicating that within a population, some individuals express morphological changes and others apparently do not express any modification.

The visible changes in global climate have altered the frequency and intensity of drought and flooding events, bringing important consequences for growth and survival of cultivated and native plants. Understanding what adaptations allow plants to respond drought stress is crucial for predicting the impacts of these climate changes in crop production and environmental dynamics (Atkin and Macherel, 2009). Since almost all plant species that comprise the Pantanal occur in other biomes whose physical environmental characteristics are distinct, populations of this biome are excellent models for studies of adaptations to stress.

2. Adaptations of the Plants of the Pantanal

The plant communities of the Pantanal are annually exposed to restrictions in obtaining resources. Thus, plants growing in low areas of Pantanal wetlands, which are called Pantanal sensu stricto areas in this study, go through the annual cycle of excess and lack of water. Typical plants from flooded fields, riparian forests, shrubs, palustrine plants and aquatic macrophytes are part of this community. Some of these species are terrestrial, and flooding is an adverse condition for them. Palustrine species, aquatic macrophytes and, among these, amphibious species, are exposed to favourable environmental conditions during the rainy season, while they face environmental constraints during the dry season.

The Pantanal sensu lato areas, with less influence of flood pulse, have flora temporarily subjected to environmental constraint, in this case, a lack of water. In high grassland areas, the excess of light and shortage of water are extreme, especially in low rainfall months. During the annual cycle, the plants located in floodable areas, such as those on flood-free soils, are subjected to a significant deviation from optimal conditions, and forced to change and respond at various functional levels of the organism, which can characterise stress (Larcher, 2004). This condition is reversible in principle, but it can become permanent and irreversible. Stress implies a loss of vitality that worsens with the duration of the event.

A lack or excess of water in the environment leads to different kinds of situations. For example, plants subjected to a process of flooding are immediately exposed to a decreased gas exchange, leading to anoxia or hypoxia conditions. This condition provokes restriction in breathing in the root system, leading to inhibition of metabolic activity and ATP production, restricting the supply of energy for root growth and causing a reduction in plant development, which leads to morphological and/or physiological changes in the organisms, in order to obtain oxygen and energy (Liao and Lin, 2001; Larcher, 2004).

On the other hand, water is also the most common limiting factor for plant growth and its lack affects the opening of the stomata, leading to reduction in photosynthetic capacity and growth rate, due to the restriction of gas exchange. Additionally, as a drought tolerance mechanism, the stomata close during the period of highest water loss, coupled with reduced internal water potential of cells through the accumulation of solutes that promote water absorption from the soil. These mechanisms allow the vegetation to survive in areas where fluid restriction is common (Larcher, 2004).

In this region, water stress suffered by different types of vegetation can be exemplified by *paratudais*, which are subjected to water deficit during the drought period and anoxia of the root system during flood. This species has different strategies to cope with hydrological variation (Soares and Oliveira, 2009), but not all groups found in the Pantanal are capable of withstanding such water variations, leading to a sequence of colonisation processes.

For example, areas previously occupied by species adapted to high water supply conditions are occupied during periods of low rainfall by pioneer woody species that colonise previously flooded grassland. According to Pott (1994), species such as *Curatella americana* L become dominant in sandy soils, while in clayey soil *Tabebuia aurea* takes over. However, when there is a series of rainy years, tree species like *Vochysia divergens* Pohl, *Licania parvifolia* Huber and *Couepia uiti* Benth., which are more tolerant to flooding, expand from patches of riparian vegetation (Pott and Pott, 2009).

Many species do not have the ability to adapt to the soil flooding process, which in turn subjects their roots to anoxic conditions, so they are indicators of the boundary between floodable and dry areas. An example is the *Caraguatá* (*Bromelia balansae* Mez), which defines areas that the flood waters reach during the rainy season. This condition is easily observed on the forest edge, where this species can survive and grow, because it is flood free.

Another interesting example can be observed in years of low flood, when *Byrsonima orbignyana* A. Juss. (Malpighiaceae), which composes the monodominant formations known as *canjiqueirais*, proliferates and colonises periodically floodable grasslands. This species has all the morphoanatomical features of xerophytes: cuticle on leaf epidermis, hypodermis aquifer, vascular bundle hem, hem extension lignified, and little intercellular space in chlorenchyma. The alternation of aquatic and terrestrial phases exposes the root system of this plant to complete anoxia or hypoxia in a given period, which may mean deviation from the ecological optimum, and results in responses that suggest the existence of an adaptive traits complex, not only structural but also physiological. This deviation is temporary, but for *B. orbignyana*, flooding exposure for prolonged periods, much higher than the annual seasonal pulse, implies a permanent injury, with the death of the individuals. Thus, even in its natural environment, this species is subject to optimum deviation, and according to Larcher (2004), this can be interpreted as a condition of stress, which is initially reversible, but can become irreversible with the prolonged duration of a flood.

The flood pulse is an annual characteristic of the Pantanal, and presents alternated multi-annual cycles, some years with predominantly high inundation and others with predominantly low inundation. This cycle shapes the landscape, "vanishing" the pioneer species that are established in the floodable grasslands in low water years. However, this condition – death of species that are intolerant to extended flood periods – is also well exemplified in Pantanal areas known as "*arrombados* of the Taquari River". In this region, extensive areas of native vegetation have been destroyed by permanent flooding, resulting in riparian forest death, caused by livestock and agriculture advancing into the high portion of this watershed in recent decades. These activities have accelerated the natural silting of the Taquari River, changing the riverbed and resulting in great losses of native vegetation areas (ANA, 2004). Interestingly, in the *arrombados* areas, terrestrial species intolerant of prolonged flooding have given way to hydrophytes, which colonise the extensive wetlands permanently.

3. Dynamics of Aquatic Plants in Relation to Seasonality

One effect of the flood is to limit the number of species per environment (Rebellato and Cunha, 2005); duration, levels and frequency of flooding are determining factors for species composition, and may act as a filter for species group. This relationship is barely known in the Pantanal; in addition, the soil fertility also contributes to species distribution. For Wang et al. (2002), intermediate levels of soil fertility tend to provide higher species richness in grasslands.

The relation between flooding and species distribution in Pantanal grasslands is poorly known, few studies have shown the species richness of these formations (Zeilhofer and Schessl, 1998; Pott and Adámoli, 1999). Periodic and pulse-type flooding of the Pantanal's low areas influences the morphological, anatomical and physiological responses (Scremin-Dias, 1999, 2000), and phenological and/or ethological adaptations, producing characteristic community structures that are not well known (Junk, 1999).

In low areas – Pantanal sensu stricto – where flooding is likely to be permanent, there is a predominance of aquatic species, which often turn into floating islands of vegetation (*baceiros*). Pivari et al. (2008) conducted a study on the dynamics of the floating islands formed by substrate histosol with variable thickness, in the Pantanal sub-regions of Miranda and Abobral. The species composition on these *baceiros* is diverse and, depending on successional stage, shrubs and small trees can grow and reproduce on them.

Aquatic plants have different life forms (Pott and Pott, 2000; Scremin-Dias, 1999, 2009), distributed along the moisture gradient. These life forms range from free floating through fixed floating, free submerged, fixed submerged, emergent, amphibious and emergent (Pott and Pott, 2000; Scremin-Dias, 2009). They correspond to the plant habit, reflecting the species' tolerance to submergence or desiccation (Scremin-Dias, 2000), and are independent of the phylogenetic correlations between groups (Scremin-Dias, 2009).

A wide inventory conducted by Pott and Pott (2000) found about 250 species of aquatic macrophytes in the Pantanal floodable areas, distributed among the phanerogams and cryptogams. Some aquatic macrophytes also form extensive monodominant areas, highlighting *pirizal* formed by *Cyperus giganteus* Vahl, the *caetezal* with prevalence of *Thalia gemiculata* L. and two species of native rice, *Oryza glumaepatula* Steud. and *O. latifolia* Desv., forming extensive rice fields along the Paraguay River.

Among these monodominant formations, *Cyperus giganteus* and *Thalia geniculata* grow preferably in areas with water level ranging up to 1.80 m at the flood peak, with water remaining in general for a short time at this level, subsequently decreasing gradually. These species tolerate palustrine soils and flood-free areas, being denominated as amphibious. The amphibious way of life is the most peculiar one, because of the ecological amplitude of the species, which grow and can reproduce in both aquatic and flood-free (aerated soils) environments.

Species with fixed floating, emergent and amphibious habits generally have stems and roots attached to the substrate. These underground parts may remain as resistance structures during the dry season (Scremin-Dias, 2009), and display contractile roots that pull the apical buds below the soil surface, protecting them during the dry season (Sculthorpe, 1967). This feature has already been described by Raunkiaer (1934) as acquired by higher plants during the evolutionary process, with the aim of hiding and protecting buds, allowing the survival of plants in unfavourable environmental conditions.

Under these conditions, various plant species express large phenotypic plasticity, an adaptation which, for Santiago and Paoli (2007), cannot be mistaken for a mere character expression in response to environmental pressures, but should be considered as a process, which is not restricted only to the individual. According to these authors, the organisms under these conditions may or may not express morphological, physiological or both traits, through gene activation or suppression, and these traits may or may not have an adaptive component.

For amphibian species, established in flood-free soil during the ebb, emergence of new stems, leaves and roots may occur, and these characteristics of the tissues are very different from those observed in individuals of the same species developed in water. Among the changes, is important to highlight the significant decrease in the leaf sheet, the petiole, the stem internodes, differential distribution of stomata and increased lignification in the vascular tissues as observed for various aquatic macrophytes in the Pantanal, accompanied by a seasonal cycle of flood and drought (Scremin-Dias, 2000, 2009).

For some species that occur in periodically flooded areas, with intensely fluctuating water levels, ecophysiological adaptations allow their "accommodation" to depth variations. This process, described by Ridge (1987), affords the elongation of petioles, leaves, stem internodes, and floral scapes, shortly after the submersion of these organisms. This, in response to anoxia, produces metabolites that act on their cells, stretching or stimulating their division, resulting in an increase in length. Thus, the distribution of species in areas with intense changes in water level favours the establishment of species that possess this adaptive mechanism.

In the Pantanal, the vast native rice fields exemplify this process. Bertazzoni (2008) measured individuals of *Oryza latifolia* with up to 5 m of stem elongation, after rising waters. According to the author, the vegetative propagation of this species is effective, because the branches drop on to the moist soil at the ebb period, allowing regrowth on the stem nodes, which stretch after the rainy season and form new individuals by budding or by seed germination. *Oryza glumaepatula* also follows the water level by elongation of stem internodes, as observed by Silva (2010) over seasonal cycles monitored in floodable fields of the Paraguay River.

4. The Evolutionary Significance of Differential Adaptations

Molecular studies have been increasingly used to evaluate adaptive differences of populations, distinguishing genetic lineages and assessing whether or not they are associated with different environments. When comparing populations that have distinct morphoanatomical characteristics, linked to their adaptation to different habitats, taxonomic and evolutionary questions arise concerning the delimitation of species. Molecular phylogenies using DNA sequences may clarify aspects of the evolution of morphological and ecological traits, and the use of multiple genes describes these processes more accurately. The comparison of homologous DNA sequences may be important in defining species of certain groups, because the observed coalescence pattern and mutational events represent the genealogical relationships, tracing the history of the ancient DNA molecule (Hewitt, 2001). Several types of molecular markers have been used, making it possible to obtain a large amount of data collected from small samples of biological material, using non-destructive methods (Petit et al., 2001).

Wu (2001) suggests that the most suitable genes to investigate processes of species differentiation are those responsible for adaptive traits. Studies in this area assess phylogenetically related species or populations, in search of different alleles that have opposite effects on adaptive value. Among the investigated genes, we can mention those related to reproduction, such as specific floral traits to different pollinator attraction (corolla color, position of anthers and stigma, odor production) (Stuurman et al., 2004) and those related to adaptation to extreme environments (Brady et al., 2005).

Plants grown under different water regimes are good models for the study of resistance genes to excess and/or scarcity of water. These plants have evolved under strong selective pressure, with leaves emerged at certain times and submerged at others. These changes have a strong impact on photosynthesis efficiency, and the genes linked to this function are strong candidates for differential adaptation. Studying the *rbcL* gene, a chloroplast gene that encodes a catalytic subunit of RuBisCO, in ecologically diverse aquatic plants, Iida et al. (2009) found positive selection in some lines with heterophylly. This increase in the aminoacid substitution rate may imply a continuous adjustment of RuBisCo over variable ecological conditions. To survive and grow under anoxia conditions, some submerged plants have to activate the transcriptional regulation of a range of genes involved in physiological events that also control energy production, pH regulation and cell growth (Harada et al., 2007). Other plants do not increase the expression of genes that optimise photosynthesis under anoxia conditions, but rather the genes related to stem elongation and metabolism of different sugars to sustain this growth (Das and Uchimiya, 2002; Harada et al., 2005). Tolerance of desiccation, as well as of water excess, induces expression of specific genes, especially genes that cause coordinated cellular metabolism suppression.

Except for cultivated plant species, the genes directly responsible for differential adaptation are rarely known. In these cases, molecular markers that represent selectively and adaptively neutral polymorphisms can be used (Durbin et al., 2003). Phylogeography, the study of spatial/temporal distribution of genetic diversity, has been widely used to assess the variability among individuals and between related species (Avise, 2000). Through this approach it is possible to identify independent evolutionary lineages and associate (or not) them with certain geographic regions, an extremely useful tool to assess whether interpopulation phenotypic differences reflect historical genetic divergence.

DNA sequencing has wide applicability in these studies because different parts of the genome have different rates of evolution, making it possible to evaluate various taxonomic levels on several geographical scales (Avise, 2000). Among the most used markers in plant phylogeography surveys, we can highlight the non-coding regions of plastid DNA (cpDNA) (Alsos et al., 2005), especially those intergenic regions that tolerate mutations and evolve rapidly without affecting the function of adjacent genes (Hamilton et al., 2003). The frequent uniparental inheritance is one of the advantages of these markers in differential assessment of pollen and seed flow (Hamilton and Miller 2002); furthermore, the analysis of cpDNA allows the identification of past hybridisation events that are not detectable morphologically (Bleeker, 2003). As the plastid genome is haploid, the effective population size is smaller than when considering the nuclear genome. This feature speeds up the genetic drift processes; hence, the cpDNA may show faster differentiation between populations or divergent lineages (Hamilton et al., 2003). Among nuclear markers, ribosomal DNA (nrDNA) is widely studied in plants. The higher plants' nrDNA is in one or more chromosomal regions, and each arrangement can display hundreds and even thousands of copies or paralogs (Buckler-IV et al., 1997). Mutations in these tandem repeats are individually homogenised through concerted evolution, in which unequal crossing-over and gene conversion are the main mechanisms involved (Arnhein, 1983). The mode and time of nrDNA concerted evolution varies greatly between different plant groups. Thus, nrDNA can present interspecific, interpopulation, and even intra-individual variation (Mayer and Soltis, 1999).

Populations with different morphoanatomical adaptations may reflect independent evolutionary units and incipient speciation processes. They may be triggered by geographical, ecological, morphological or behavioral changes, with natural selection and genetic drift being the most active evolutionary mechanisms. To understand these processes and to distinguish phenotypic plasticity from genetic differentiation, it is interesting to approach the morphological characteristics in a genetic context, obtained through neutral or adaptive molecular markers. Evaluating these patterns of several Pantanal species, we will be able to outline a more complete overview on the phytoecological evolution of this biome.

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Ethnobotany and traditional medicine of the inhabitants of the Pantanal Negro sub-region and the raizeiros of Miranda and Aquidauna, Mato Grosso do Sul, Brazil

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(With 1 figure)

Abstract

A survey on the use of medical plants was carried out in the rural communities of the Rio Negro sub-region of the Pantanal and the *raizeiros* from Aquidauana and Miranda municipalities, Mato Grosso do Sul, Brazil, in order to recover the ethnobotanical and ethnopharmacological knowledge of these communities. Structured questionnaires were run with the residents of eight farms and 12 *raizeiros*. The results reveal 25 botanical families, 45 genera and 48 species of medicinal plants used, six of which are indicated for kidney disturbances, six for urinary disturbances, five for inflammation treatment, 13 for stomach aches, 10 for respiratory disturbances, four for treating sprains, four for healing wounds, four as anti-diarrheaic and one as antipyretic, among other illnesses. The main family was Asteraceae, with 12 species used. The principal preparation methods of the medicinal herbs in the Rio Negro sub-region and surrounding areas were infusion (35) and, mostly, mixed with "chimarrão" or "mate quente", traditional beverage. Nineteen exotic species are used by the *raizeiros*, (39.58%), which indicates a strong influence of the urban environment. The traditional *pantaneiros* have greater knowledge of medicinal plants than the *raizeiros*, and they cited only five exotic species (16.1%).

Keywords: folk medicine, medicinal plants, ethnopharmacology.

Etnobotânica e medicina tradicional dos habitantes da sub-região do Pantanal do Negro e raizeiros das cidades de Miranda e Aquidauana, Mato Grosso do Sul, Brasil

Resumo

Foi realizado um levantamento sobre o uso de plantas medicinais junto às comunidades rurais, da sub-região do Rio Negro e raizeiros das cidades de Aquidauana e Miranda, Mato Grosso do Sul, Brasil. O objetivo foi resgatar o conhecimento etnobotânico e etnofarmacológico dessas comunidades, por meio da aplicação de questionários a moradores de oito fazendas e 12 raizeiros. Os resultados indicaram a utilização de 25 famílias, 45 gêneros e 48 espécies de plantas medicinais, sendo seis utilizadas para afecções dos rins, seis para tratamento das vias urinárias, cinco no tratamento de inflamações, 13 para dores estomacais, quatro como cicatrizantes, 10 para afecções do aparelho respiratório, quatro para todo o tipo de torções, quatro como antidiarreicas e uma no combate às febres, entre outras doenças. A principal família utilizada é Asteraceae, com 12 espécies. As principais formas de utilização das plantas são os chás por infusão (citado 35 vezes), isoladamente ou com as partes da planta misturadas no mate quente ou chimarrão, bebidas tradicionais da região pantaneira. O número de espécies exóticas utilizadas, 19 (39,58%), indica forte influência das correntes migratórias para a região, o que pode comprometer a médio e longo prazos, o conhecimento das populações locais. Os pantaneiros tradicionais têm maior conhecimento sobre as plantas medicinais nativas do que os raizeiros das cidades de Miranda e Aquidauna, citando apenas cinco espécies exóticas (16,1%).

Palavras-chave: medicina popular, plantas medicinais, etnofarmacologia.

1. Introduction

The use of plants in the treatment of several diseases is reported in different populations (e.g., Berg and Silva, 1988; Bird, 1991; Verger, 1995; Guarim-Neto, 2006; Kunwar et al., 2006). The knowledge of medicinal plants often represents the only therapeutic option for many communities and ethnic groups. Revene et al. (2008) point out that traditional medicine in poor countries is the most accessible practice and, in certain situations, the only treatment available.

According to Maciel et al. (2002), the use of plants to treat and cure diseases is as old as the human species and today in the poorest regions of the country and even on the outskirts of large Brazilian cities, medicinal plants are sold in street markets and fairs and found in the backyards of residences. The World Health Organization (WHO) states that approximately 80% of the population use traditional medicine in primary health care (WHO, 2002). The discovery and disclosure of medicinal flora properties, through the knowledge of traditional populations, is, therefore, an important tool in preserving the cultural richness of different regions.

In Brazil, the use of herbs for medicinal purposes is a widespread practice, enhanced by cultural differences, deriving from colonisation by the European and African populations, in addition to traditional indigenous knowledge (Gomes et al., 2008). According to Martins et al. (2000), the use of plants to treat diseases has, fundamentally, influences from several different cultures that include the Indians who use phytotherapy in a mystical way: the shaman or witch doctor of the tribe often uses herbs with narcotic and/or hallucinogenic effects to dream about spirits. These reveal the herb or the procedure to be followed to cure the sick person, or the shaman may observe animals that look for certain plants when they are sick. Black populations descended from African slaves have also introduced new species with curative intent, seeking to "expel" the disease through rituals and natural products, including those of animal origin.

This mixture of traditions, associated with the high plant diversity in Brazil, has led to a traditional medicine based on different plants and methods of treatment and researchers (e.g., such as Correa, 1926-1978; Rizzini and Mors, 1976; Berg, 1993; Ming, 1995; Agra, 1996) demonstrate the richness of medicinal flora in different Brazilian regions.

Among the Brazilian biomes, the Pantanal is a region with associated vegetation formations and, according to Pott and Pott (1994), the colonisation of species from regions like Chaco, Cerrado, Amazon and Atlantic forest has allowed the occurrence of wide distribution species and low endemism. Alho (2008a,b) and Oliveira (2007, 2008) affirm that each sub-region of Pantanal wetland (a periodically flooded area), shows vegetation characteristics associated with different environmental factors such as soil type, flood level and slope, which influence species distribution and provide great floristic diversity.

Thus, this biome is an important vegetation complex for the study of medicinal herbs, covering a diversity of species with great potential for ethnobotanical studies (e.g. Conceição and Paula, 1986; Pott and Pott, 1994; Bortolotto, 1999; Souza and Guarim-Neto, 1999; Pott and Pott, 2000; Schwenk and Silva, 2000; Campos Filho, 2002). It is also occupied by a native population with great cultural importance, adapted to the intermittent cycles of flood and drought of the region, the *pantaneiros* or marsh-dwellers (Nogueira, 2002).

The use of plants for therapeutic purposes in the Pantanal region has long been reported in various Indian tribes. Since the first colonisation of the region, especially during the Paraguay War (1864-1870), extractivist activities have been intensified in other communities and are now part of the '*pantaneiros*' lives, either for medicinal ends or just to bring comfort in the face of their daily adversities (WHO, 2002).

The knowledge of the correct use of plant species normally belongs to restricted groups of the population, known as *raizeiros* (generally people with little formal education, who through the knowledge transmitted by their parents or other people with empirical knowledge, use plants for disease treatment), *benzedeiras* (usually women, who treat distinct diseases through prayer and herbs) and other, usually elderly, people, who received medicinal information from their ancestors (Guarim-Neto, 2006). As these groups are restricted and often threatened by environmental changes, which alter their lifestyle and culture, the recovery of this ethnobotanical knowledge is fundamental in rescuing traditions that may soon be lost.

Considering the information gaps in the ethnobotanical and ethnopharmacological knowledge of the traditional *pantaneiros* from Rio Negro sub-region and the *raizeiros* of the municipalities of Aquidauana and Miranda, this work aims to identify the plants used in folk medicine and their respective utilisation.

2. Material and Methods

This study was conducted with 14 traditional residents of eight farms (Santa Emilia, Chão Parado, Conquista, Santa Maria, Campo Lourdes, São Roque, Bandeirantes and Santa Marta) near the city of Aquidauana, and with twelve *raizeiros*, six from the urban area of Aquidauana and six of Miranda municipalities, located at the edge of the southern Pantanal, Mato Grosso do Sul, Brazil (Figure 1).

These towns are directly influenced by the Pantanal region. They have a large rural-origin population and, for this reason, were chosen to be the interview set.

A structured questionnaire (popular name, preparation method and therapeutic indications) was developed and applied in march-october/2008, in order to define a profile of the traditional *pantaneiros* and *raizeiros*, concerning their experience and knowledge of the therapeutic usage of medicinal plants. The species cited by Sano and Almeida (1998) and Pott and Pott (1994, 1999) were considered

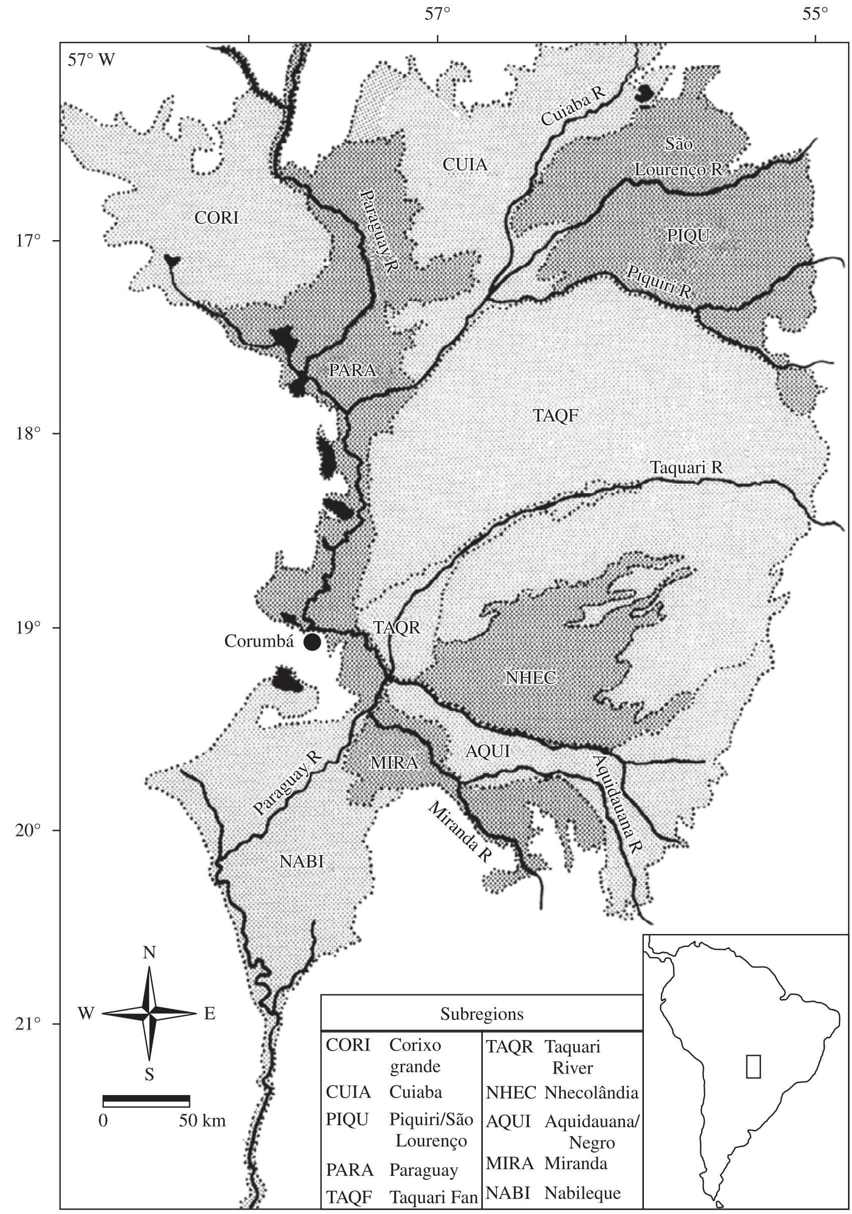

Figure 1. Map of the Pantanal wetland, showing the 10 subregions, by Hamilton et al. (1996).

native to the region, and Lorenzi and Matos (2002) were also consulted.

In this study, the interviews were designed for people born in the Pantanal region or who have spent most of their lives in the region, and interacted with the environment through the use of natural resources as a way of survival. To avoid embarrassment, the interviewees were free to speak according to their own situation and the interviews were carried out using regional language.

The species mentioned by the *pantaneiros* and *raizeiros* were collected in the indicated areas by the interviewees, and transported to the Anhanguera-Uniderp University herbarium for identification and deposit. The classification system used was APG II (Angiosperm Phylogeny Group, 2003).

3. Results and Discussion

In the present study 25 families, 45 genera and 48 species of medicinal plants of routine use were identified, 19 of which were exotic species (introduced in the region) and 29 (60.42%) were native (Table 1). The family with largest number of used species was Asteraceae (12), followed by the family Lamiaceae (7).

The herb "boldo" (*P. barbatus*), an introduced species, was the most cited (seven times), which indicates the strong

Table 1. Family, popular and scientific name, citation number (CN) – "Pantaneiros" (P) and "raizeiros" (R), preparation method (PM), therapeutic indications (TI) and origin of the medicinal plants cited by the *raizeiros* of the municipalities of Aquidauana and Miranda and by the traditional *pantaneiros* of the Rio Negro sub-region, Pantanal, Mato Grosso do Sul, Brazil.

Family	Popular and scientific name	CN	PM	TI	Native species
Adoxaceae	Sabugueiro - *Sambucus australis* Cham. & Schltdl.	1 - P	Infusion	Measles and fever	Yes
Amaranthaceae	Terramicina, Chapéu de couro (Cabeça-branca), Estomalina - *Alternanthera brasiliana* (L.) O. Kuntze	1 - R 1 - P	Poultice (2) Infusion (1)	Wounds (2) Stomach aches (1)	Yes
	Erva-de-Santa Maria ou mastruz - *Chenopodium ambrosioides* L.	3 - R 2 – P	Smoothie	Vermifuge	Yes
Arecaceae	Coco da Bahia - *Cocos nucifera* L.	R - 1	Infusion	Hepatitis	No
Asteraceae	Anador - *Artemisia verlotorum* Lamotte	2 - R 2 - P	Infusion	Pains	Yes
	Chifre-de-carneiro - *Acanthospermum hispidum* DC.	1 - R 1 - P	Infusion	Diuretic/ kidney disturbances	Yes
	Picão - *Bidens pilosa* L.	2 - R 1 - P	Infusion	Verminosis	Yes
	Arnica - *Lychnophora ericoides* Mart.	2 - R 1 - P	Poultice	Healing/ Pains	Yes
	Caferana - *Vernonia polyanthes* Less.	1 - P	Infusion	Stomach aches	Yes
	Guaco - *Mikania laevigata* Schultz Bip. ex Baker	1 - R	Infusion	Cough	Yes
	Camomila - *Chamomilla recutita* (L.) Rauschter	1 - R	Infusion	Colic and sedative	No
	Cravo-de-defunto - *Tagetes patula* L.	1 - R	Infusion	Pneumonia	No
	Carqueja - *Baccharis articulata* (Lam.) Pers.	1 - R	Infusion	Stomach aches	Yes
	Assa-peixe – *Vernonia ferruginea* Less.	1 - P	Infusion	Cough/ Snoring	Yes
	Erva de Luceira - *Pluchea sagittalis* (Lam.) Cabrera	2 - R 1 - P	Poultice	Wounds/ Sprains	Yes
Bignoniaceae	Piúva - *Tabebuia heptaphylla* (Vell.) Tol.	1 - P	Infusion	Inflammation	Yes
	Paratudo, Ipê - *T. aurea* (Manso) Benth. & Hook. f. ex. S. Moore	1 - R 2 - P	Decoction (1) Infusion (2)	Bronchitis/ Inflammationand several different ailments Stomach	Yes
Celastraceae	Cancorosa - *Maytenus* cf. *macrodonta* Reiss.	1 - P	Infusion	Infection	Yes
Crassulaceae	Saião - *Kalanchoe brasiliensis* Camb.	1 - P	Chew the leaf	Stomach aches	No
Curcubitaceae	Melão-de-São-Caetano - *Momordica charantia* L.	1 - P	Poultice	Healing	No
Euphorbiaceae	Quebra-pedra - *Phyllanthus amarus* K. Schum.	1 - R 2 - P	Infusion	Kidney stones	Yes

Table1. Continued...

Family	Popular and scientific name	CN	PM	TI	Native species
Fabaceae	Fedegoso - *Senna occidentalis* (L.) Link	1 - R 3 - P	Cold tea	Stimulant/ Verminosis	Yes
	Amargoso - *Vatairea macrocarpa* (Benth.) Ducke.	1 - P	Infusion	Stomach/ Liver	Yes
Lamiaceae	Boldo - *Plectranthus barbatus* Andr.	4 - R 3 - P	Maceration/ Cold tea	Digestion	No
	Boldo (Boldo do Chile) - *P. neochilus* Schlechter	1 - P	Infusion	Head and stomach aches	No
	Erva cidreira - *Melissa officinalis* L.	2 - R 1 - P	Infusion	High pressure and insomnia	No
	Poejo - *Mentha pulegium* L.	2 - R	Infusion	Flu	No
	Hortelã do campo - *Hyptis crenata* Pohl ex Benth.	1 - R	Infusion	Vermifuge	Yes
	Alecrim - *Rosmarinus officinalis* L.	2 - R	Infusion	Heart disturbances	No
	Hortelã gorda - *Mentha x piperita* L.	1 - P	Infusion	Stomach aches	No
Lauraceae	Abacateiro - *Persea americana* Mill.	1 - R	Infusion	Urinary disturbances	No
Lytraceae	Romã - *Punica granatum* L.	1 - R	Infusion	Gastritis	No
Malvaceae	Malva branca - *Waltheria communis* A. St.-Hil.	2 - P	Infusion	Wound asepsis	Yes
Nyctaginaceae	Amarra-pinto - *Boerhavia diffusa* L.	1 - R	Infusion	Infection/ Diuretic	Yes
Piperaceae	Pariparoba - *Piper regnellii* (Miq) C. DC.	2 - P	Infusion	Stomach	Yes
Plantaginaceae	Vassourinha - *Scoparia montevidensis* (Spreng.) R. E. Fries	2 - P	Infusion	Renal pains	Yes
Poaceae	Capim amargoso - *Setaria poiretiana* (Schult.) Kunth.	1 - P	Poultice	Healing	Yes
	Capim cidreira - *Cymbopogon citratus* (D.C.) Stapf	1 - R 1 - P	Infusion	Sedative	No
Polygonaceae	Erva-de-bicho - *Polygonum hydropiperoides* Michx.	1 - P	Poultice	Wound asepsis/ Chilblain	Yes
Rubiaceae	Congonha de bugre - *Rudgea viburnoides* (Cham.) Benth.	2 - P	Infusion	Heart disturbances/ kidney	Yes
Rutaceae	Arruda - *Ruta graveolens* L.	1 - R	Infusion	Menstrual colic pains	No
	Laranjeira - *Citrus aurantium* var. Dalmau	1 - R	Infusion	Pains/ flu	No
Solanaceae	Beladona - *Atropa belladonna* L.	1 - R	Hot Poultice	Twist pains	No
	Juá - *Solanum viarum* Dun.	1 - R 2 - P	Infusion	Kidney	Yes
	Tomate cereja - *Solanum lycopersicon* L.	1 - R	Maceration/ Cold Tea	Kidney disturbances	No
Teophrastaceae	Erva de bugre - *Clavija nutans* (Vell.) Stahl.	1 - P	Infusion	Flu	Yes
Verbenaceae	Gervão - *Stachytarpheta cayennensis* (Rich.) Vahl	1 - R 1 - P	Ointment	Healing	Yes
Xanthorrhoeaceae	Babosa - *Aloe arborescens* Mill.	1 - R	Hot poultice	Pneumonia	No

influence of exotic species on the local culture. Successively, the most remembered herbs were "erva-de-santa Maria" or "mastruz" (*C. ambrosioides*) (5), "anador" (*A. vermolotorum*) and "fedegoso" (*S. occidentalis*) (4), "juá" (*S. viarum*), "picão" (*B. pilosa*), "arnica" (*L. ericoides*), "quebra-pedra" (*P. amarus*) and "erva cidreira" (*M. officinalis*) (3).

Most of the interviewees (35-71.4%) carry out infusion preparations with the herbs, pouring hot water over selected parts of them and letting them steep for a few minutes. The medicinal herbs can be also added to "chimarrão" or "mate-quente", a traditional hot beverage prepared from steeping dried leaves of *Ilex paraguariensis* A. St.-Hil. This hot beverage is normally drunk when neighbours or friends gather in the early morning or late afternoon to talk about daily issues, forming a particular social setting known as "rodas de prosa".

The latter method is commonly used by the population, due to easy handling of the medicinal plants, uniting the traditional habit of drinking "chimarrão" with the necessity of treating the sick.

The use of medicinal herbs in the states of Mato Grosso and Mato Grosso do Sul is reported by different researchers. Berg (1980) conducted a study in the cities of Cuiabá and Chapada dos Guimarães, Mato Grosso, and reported 103 species used for medicinal purposes. Guarim-Neto (2006), in a compilation of his earlier research, reveals that 56 medicinal plants are used in the traditional medicine practices of *pantaneiros*, eight more than those reported for the Rio Negro sub-region.

Berg and Silva (1988) performed a survey in the cities of Campo Grande, Aquidauana and Miranda, and in the Pantanal of Mato Grosso do Sul State, in which they listed 104 species considered as medicinal flora. Compared with the data obtained in the present study, 41 species identified in this research were not reported by Berg and Silva (1988).

The Aquidauana and Miranda *raizeiros* named 33 species, 16 of them exotic (Table 1), such as "abacateiro" (*P. americana*), "boldo" (*P. barbatus*), "erva cidreira" (*M. officinalis*), "erva-de-Santa Maria" (*C. ambrosioides*), "picão" (*B. pilosa*), "romã" (*P. granatum*), among others.

The information obtained indicates that *raizeiros* interviewed are former residents of rural areas, who moved to the towns to seek a better life. However, they still keep up rural customs, cultivating herbs in the backyard, even when living close to pharmacies. These recent urban residents utilise natural medicine routinely, and share their vast knowledge of medicinal herbs with neighbours and close relatives. However, it was observed that the longer they had lived in the town, the greater was the difficulty to list a significant number of species that had been used in their previous rural life.

Furthermore, 39.58% of the species mentioned by the *raizeiros* are exotic, which indicates the strong influence of the urban environment on the utilisation of medicinal flora and the gradual loss of any connection with the rural environment and its medicinal species. The exotic species "boldo" (*P. barbatus*) was the most mentioned; this species is indicated for stomach aches and as digestive stimulant, similar results found by Guarim-Neto (1984) and Berg (1980). According to Costa et al. (2003), studies revealed that "boldo" has hypotensive, vasodilation, gastric hyposecretory, blood pressure reducing anti-dyspeptic properties. The second most cited species was "erva-de-Santa Maria" (*C. ambrosioides*) (native), used as a vermifuge. The medicinal use of this species is widespread, showing stomachic, anti-rheumatic and anthelmintic properties. "Alecrim" (*R. officinalis*), "anador" (*A. vermolotorum*), "arnica" (*L. ericoides*), "capim cidreira" (*C. citratus*), "picão" (*B. pilosa*) and "poejo" (*M. pulegium*) were mentioned three times; they are all commonly used in folk medicine, except for "arnica" (Lorenzi and Matos, 2002). The others species were cited only once.

Regarding the answers of traditional *pantaneiros*, 31 medicinal species were cited (Table 1), with only five exotic ones (16.1%), indicating a strong link with the local flora and little external influence on medicinal herb use.

"Boldo" also shows a higher frequency of citations (three), together with "fedegoso" (*S. occidentalis*), used in phytotherapy as a stimulant, vermifuge and against anemia. The literature demonstrates that organic extracts of *S. occidentalis* have purgative, hepatic, antibacterial, antipyretic, antitumor, expectorant, anti-inflammatory, diuretic, antifungal and neurotoxic properties for cattle (Viegas et al., 2006). The species with only two citations were "anador" (*A. vermolotorum*), "congonha de bugre" (*R. viburnoides*), "erva-de-Santa Maria" (*C. ambrosioides*), "juá" (*S. viarum*), "malva branca" (*W. communis*), "paratudo" (*T. aurea*), "pariparoba" (*P. regnellii*), "quebra-pedra" (*P. amarus*) and "vassourinha" (*S. montevidensis*), commonly used in Brazilian folk medicine (Lorenzi and Matos, 2002; Guarim-Neto, 2006).

There are 13 species common to both localities, such as "anador" (*A. vermolotorum*), "arnica" (*L. ericoides*), "boldo" (*P. barbatus*), "capim cidreira" (*C. citratus*), "juá" (*S. viarum*), "picão" (*B. pilosa*) and others, with the smallest portion of exotic species (4-30.8%). The traditional *pantaneiros* apparently have a greater knowledge of native medicinal plants than the *raizeiros* (residents of urban areas), who mentioned a representative number of exotic plants.

The knowledge of native plants is getting lost in the Pantanal region, due to neglect of the '*pantaneiros*' traditional values, their migration to urban areas and contact with new immigrants arriving in the region. The recovery of this empirical knowledge is important for biodiversity conservation, to create alternatives for subsistence livelihoods and to maintain cultural diversity.

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Coleoptera (Insecta) as forest fragmentation indicators in the Rio Negro sub-region of the Pantanal, Mato Grosso do Sul, Brazil

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Abstract

The purpose of this study was to evaluate the integrity of two forest fragments in Rio Negro Pantanal sub-region, using coleopterans as environmental indicators. The study was carried out at Santa Emilia Farm in the Rio Negro sub-region, municipality of Aquidauana, Mato Grosso do Sul (19º 30' 18'' S and 55° 36' 45'' W). Two sites were selected, locally denominated as "cordilheiras" (narrow and elongated strands of elevated soil), one with low degree of anthropic disturbance (CL) and the other, currently undergoing restoration process (TD). The sampling sites were determined using a GPS device. Ten pit-fall traps containing water and detergent were used for the specimens sampling, which were screened and identified. Abundance, richness, diversity and similarity were determined. Abundance was higher for CL (n = 277) than for TD (n = 251). The same was observed for the diversity indices, CL showed H' = 2.83 $bit.individual^{-1}$ and TD = 2.48 $bit.individual^{-1}$, confirming the interferences made for abundance. Specimens of ten families were captured in CL area and seven families in TD area, indicating higher richness in CL, when compared to TD. The linear correlation coefficient ($p > 0.05$) indicates that both areas are significantly different, showing similarity value of 66.7%. The data show that the structure and disturbance degree in the environment integrity influence the composition of beetles fauna, causing the increase of abundance, richness and diversity in anthropogenic environments undergoing the early stage of regeneration.

Keywords: biodiversity, flood plain, insects, coleopterans.

Coleoptera (Insecta) como indicadores de fragmentação florestal na sub-região do Pantanal do Negro, Mato Grosso do Sul, Brasil

Resumo

Este trabalho avalia a integridade de dois fragmentos de floresta da sub-região do Rio Negro do Pantanal, utilizando coleópteros como indicadores. O estudo foi conduzido na Fazenda Santa Emília, na sub-região do Rio Negro, município de Aquidauana, Estado de Mato Grosso do Sul (19º 30' 18'' S e 55° 36' 45'' W). Dois estreitos fragmentos de floresta (localmente conhecida com cordilheira), situados em terrenos um pouco mais elevados, um com baixo grau de perturbação antrópica (CL) e o outro em processo de restauração (TD). Os sítios de amostragem foram marcados com GPS. Dez armadilhas de queda contendo água e detergente foram utilizadas. Abundância, riqueza de espécie, diversidade e similaridade foram determinadas. Abundância foi maior para CL (n = 277) do que para TD (n = 251). A mesma tendência foi observada para índices de diversidade, CL com 2,83 e TD com 2,48. Indivíduos de dez famílias foram capturados na área CL e de sete famílias na área TD, indicando mais alta riqueza em CL. O coeficiente de correlação linear ($p > 0,05$) indica que ambas as áreas são significantemente diferentes, com valor de similaridade de 66,7%. Os dados mostram que o grau de perturbação e estrutura da integridade ambiental influencia a composição da fauna de besouros, causando o aumento em abundância, riqueza e diversidade nos dois fragmentos estudados.

Palavras-chave: biodiversidade, planície de inundação, insetos, coleópteros.

1. Introduction

A forest fragment can be defined as "any area of continuous natural vegetation, interrupted by anthropic barriers (roads, agricultural crops, etc.), or natural ones (lakes, other vegetation types, etc), capable of significantly reducing the flow of animals, pollen, and/or seeds" (Tabanez et al., 1997). The structure and dynamic of forest fragments vary depending on several factors, mainly the history of disturbance, the area's shape, the type of neighbouring environments and the isolation degree and, depending on these characteristics, can be self-sustaining or not (Tabanez et al., 1997).

Struminski and Lorenzotto (2003) emphasises the obvious importance of knowledge about fragmentation nowadays, because in many landscapes vast numbers of species are restricted to fragments. In the State of Mato Grosso do Sul, there is a typical ecosystem, popularly known as "*Pantanal*", with landscapes formed by complex of natural environments or habitats that comprise a set of natural forest fragments interspersed among ponds ("baías"), drainage channels ("vazantes" and "corixos") and rivers, forming a landscape mosaic.

In this region there are different vegetation physiognomies such as areas with riparian and gallery forests, savannas (forested, wooded and open grassland sub-types) which have several regional denominations such as "capões", "cordilheiras", "cambarazais", "paratudais", among others. Normally, these phytophysiognomies are not extensive, being interspersed with other landscape types. The gradient of forested, wooded, shrub and grassland formations is determined by topography, edaphic factors and mainly seasonal conditions like the dry and wet periods, because annual flooding, when more than 50% of the region is covered by water, contributes significantly to the formation of these environments (Magalhães, 1992).

The understanding of the biological dynamics of these habitats contributes to the comprehension of the Pantanal biome as a whole, allowing a diagnosis of the behaviour of certain species in existing forest fragments. One of the more accessible groups to this type of study, already used as environmental quality indicators, is that of entomofauna (Freitas et al., 2003).

Alho (2003) describes indicators as signs or evidences that enable researchers to verify the amplitude of variations which the observed phenomenon is suffering, due to specific processes or interventions. Therefore, various types of indicators can be established: context indicators – when is desired to monitor events or situations related to a wide region; process indicators - when what becomes important is the observation of the actions sequence or behaviour interactions, in a time scale; impact indicators - when the purpose is to check the effects pertinent to general goals, such as the number of species in an area designated for monitoring.

The use of indicator species to assess and monitor biological processes in the ecosystems dates from the early twentieth century. Later this concept was largely developed for the utilisation in pollution control in rivers and lakes. It is based on the use of species present in the community and subjected to some kind of evolutionary impact, in the past, or anthropogenic impact in the present (Correia, 2002).

Due to its biological importance, entomofauna is normally used as an evaluation parameter of fragmented areas. This group is one of the most important, because they comprise about 59% of all existing animals (759,000 species formally described), however they have been rarely used as "flagship species" in the conservation of natural areas. Although birds and mammals are most appreciated by conservationists in general, the usefulness of insects as environmental indicators is unquestionable. Some groups, among which butterflies, beetles and ants, are especially useful in environmental monitoring since they are easily sampled and identified, found all year round, and show fast response to environmental changes. Therefore, they can provide more information than vertebrates in general, due to their great usefulness in characterising small fragmented areas or with a long history of anthropogenic influence habitats, where many of the most sensitive and large vertebrates have already been eliminated by the reduction in living and hunting areas (Freitas et al., 2003).

Insect diversity influences ecosystem dynamics through numerous mechanisms such as litter decomposition, pollination, growth suppression of plants or serving as prey to carnivores. According to their role in ecosystem dynamics, these invertebrates are classified in three categories: explorers, acting as herbivores, parasitoids or predators; suppliers, serving as hosts to parasitoids or preys to predators; and facilitators, acting as pollinators, pathogen vectors or phoresy (Thomazini and Thomazini, 2000).

Regarding the choice of key insect groups for studies in fragmented forest systems, the most important ones are those capable of inducing physical changes in their environment and regulate the availability of resources to other species, such as pollinators, seed predators, parasitoids and decomposers (Didham et al., 1996).

Among these groups, the beetles of the family Scarabaeidae (Coleoptera) are used as indicators in studies on diversity of insects or arthropods and considered essential in studies on forest fragmentation, since much of the food (feces and carcasses) of this group is produced by organisms strongly affected by this process, such as birds, primates and other large mammals (Lovejoy et al., 1986). Furthermore, they are important in soil nutrients recycling, in the control of parasites of some vertebrates and in seed dispersal (Klein, 1989). The utilization of these beetles as indicators in biodiversity survey programmes has also been suggested, owing to the great morphological, taxonomic, ecological and behavioural variability, sensitivity to environmental changes and abundance (Thomazini and Thomazini, 2000).

Accordingly, this study aims to evaluate the integrity of forest fragments in the Rio Negro Pantanal sub-region, using Coleoptera species as environmental indicators.

2. Material and Methods

The study was conducted at Santa Emilia Farm (Rio Negro Pantanal's sub-region), municipality of Aquidauana, Mato Grosso do Sul, 270 km from Campo Grande, where the Instituto de Pesquisa do Pantanal – IPPAN, of Universidade para o Desenvolvimento do Estado e da Região do Pantanal – UNIDERP, is situated. In this area there is a diversity of environmental conditions, with a large variety of vegetation types including riparian and gallery forests, which occupy large areas along the "Correntoso River", and the typical forests of "cordilheiras", narrow and elongated strands of elevated soil (1-2 m) above floodable grasslands. It has been suggested that they are ancient dunes covered by "cerradão" vegetation (forested savanna), presenting tall trees (12-16 m) and shorter ones (3-7 m) (Alho and Gonçalves, 2005).

The woody vegetation of this formation, with its sandy soil, has typical species, with emphasis on the occurrence of "Cambará" (*Volchysia divergens,* Pohl), "Tarumã" (*Vitex cymosa* Bertero), "Jatobá mirim" (*Hymenaea* sp. L.), "Ximbuva" (*Enterolobium* sp. Mart.), "Novateiro" (*Triplaris americana* L.), "Paratudo" (*Tabebuia aurea* (Manso)), "Manduvi" (*Sterculia apetala* (Jacq)), "Piuva" (*Tabebuia* sp. Gomes ex D.C.), "Gonçalo" (*Astronium fraxinifolium* Scott), "Embaúba" (*Cecropia pachystachya* Trec.), "Acuri" (*Attalea phalerata* Mart.), "Figueiras" (*Ficus* sp. L.), "Pequi" (*Caryocar brasiliense* L.), "Bocaiúva" (*Acrocomia aculeata* Jacq.), "Lixeira" (*Curatella americana* L.), "Cumbaru" (*Dipteryx alata* Vog.), "Maminha-de-porca" (*Zanthoxylum rigidum* Humb). In the shrub stratum, the presence of representatives of the families Rubiaceae and Myrtacea was registered, among others (Pott and Pott, 2003). In the vicinity of the "cordilheira", natural grasslands are encountered constituted by "capim barba-de-velho" (*Pterocaulon virgatum* D.C.) and "capim navalha" (*Scleria melaleuca* Rchb. ex Schltdl. & Cham.), where scattered clumps of "Canjiqueiras" (*Birsonima* sp Rich ex Kunth.) are found.

For the field work execution and data sampling, two sites with low anthropogenic influence and 3,096.42 m apart from each other were previously established. In the past, selective extractions of wood were undertaken in these locations, but are currently undergoing advanced regeneration process.

The first site is located near the region locally known as "baía do cervo", which is bordered by a "cordilheira" that received the denomination "Cordilheira das Três Divisas" (TD), located at 19° 30' 23'' S and 55° 35' 32'' W.

The second site is located near the Santa Marta Farm boundary, in a "cordilheira" that received the denomination "Cordilheira do Lau" (CL), located at 19° 29'' 24'' S and 55° 36' 38'' W.

The sampling effort was undertaken through the installation of 10 pit-fall traps, containing water and detergent, and the captured insects were collected at dawn (Almeida et al., 1998). Four sampling sessions were performed.

The sampled specimens were stored in glass bottles properly covered and containing ethylic alcohol (70%), which were labelled (date, sampling place and time) and transported to the Entomology Lab of Anhanguera-Uniderp University for screening, taxonomic identification and, then, deposited in the scientific collection. Statistical treatment was performed to determine the abundance, richness (jackknife1), diversity (Shannon index, log 10), similarity (SØrensen) and evenness of the species occurring in the sampling sites (Krebs, 1989).

3. Results and Discussion

3.1. Abundance and diversity

In this study, 528 coleopterans distributed in 10 families were collected. The largest number of specimens (277) was captured in the area denominated "Cordilheira do Lau" (CL), and the lowest number in "Cordilheira das Três Divisas" (TD) (251) (Table 1).

Abundance was higher in CL, which demonstrates the advanced restoration degree of the vegetation compared to the TD area. The greater abundance in the CL area is due to the higher number of species of the family Scarabaeidae (13) collected during the four samplings and also to the significant occurrence of the species 5 of Scarabaeidae (134) in the first sampling in CL area (Table 1). These insects help in dispersal and burial of seeds, with potential long-term effects on forest maintenance or restoration (Lewinsohn et al., 2005). Similar results were obtained by Marinoni and Ganho (2003, 2006) and Ganho and Marinoni (2003) in anthropogenic areas of Araucaria in the state of Paraná.

These numbers may be associated with the greater diversity of feeding habits of the coleopterans and to the greater availability of floristic resources in regeneration areas. The elevated number of individuals of certain plant species leads to large production of fruits, that attract specific coleopterans and mammals that feed on them, leaving in place large amount of feces, which also attract other organisms. Hutcheson (1990) mentions that in more open habitats at the climax stage and dominated by shrubs, fewer individuals were captured comparing to restoration areas, in the same ecosystem type.

This feature can also be observed when comparing the diversity indices calculated for each studied area, CL showed H'= 2.83 bit. individuals^{-1} and TD H'= 2.48 bit.indivíduo^{-1}, confirming the inferences made for abundance (Table 2).

3.2. Family richness

Ten families were found in the CL area and seven families in TD, consequently CL showed greater family richness (Tables 1 and 2).

Regarding the Brazilian coleopterofauna, Costa Lima (1952) listed 112 families, Costa et al. (1988) listed 109 families, and Costa (1999) 106 families. This variation is an outcome of constant revisions of the coleopterans classification. In the present work, the low family richness found is probably due to the sampling method, since the attractants, baits or lures were not used in the traps, which were randomly installed in the studied areas.

The greatest richness in CL can be explained by the highest productivity of this area, that displays regeneration degree with higher regrowth, flowering and leaves and fruits falling, that provide resources for phytophagous species, besides the presence of feces and carcasses resulting from the native mammalian fauna (feral pigs, capybaras, tapirs, primates) and birds. Agropastoral activity within and in the surrounding area also serves as a resource for necrophagus and coprophagus species, which feed on these ruminants feces as explained by Thomazini and Thomazini (2000). Therefore, it is possible to observe that the difference between the areas may be conditioned by the presence of rare individuals and not by the degree of preservation, as affirmed by Ganho and Marinoni (2003).

Table 1. Families of Coleoptera collected in two "cordilheiras" of Rio Negro Pantanal sub-region, Santa Emília Farm, Mato Grosso do Sul.

Taxon	Morphotype	TD[1]	CL[1]
Bruchidae	1	0	1
Carabidae	1	9	4
	2	63	44
	3	1	2
	4	1	1
	5	0	1
	6	2	1
	7	0	4
	8	1	1
Cerambycidae	1	0	1
Chrysomelidae	1	3	3
	2	2	2
	3	1	1
	4	0	1
Curculionidae	1	18	11
	2	9	3
	3	1	0
Histeridae	1	1	1
Nitidulidae	1	0	2
	2	1	3
Staphilinidae	1	0	3
Scarabaeidae	1	118	33
	2	1	1
	3	11	9
	4	5	2
	5	0	134
	6	0	1
	7	0	1
	8	0	1
	9	0	1
	10	0	1
	11	0	1
	12	1	1
	13	1	0
Tenebrionidae	1	1	0
	2	0	1
Total	-x-	251	277

1/TD = "Cordilheira das Três Divisas"; CL = "Cordilheira do Lau".

3.3. Community structure

Similarity

The structures of coleopteran communities in the TD and CL areas, based on the total values of species abundance, are not significantly similar (linear correlation coefficient $p > 0.05$) (Table 2).

Both sampling areas demonstrate independent community structure, showing 66.7% similarity, due to the approximate number of species richness in each area, associated to the proportionally low number of shared species (17 species of the 54 registered) (Table 1). Considering that the physiognomic characteristics of the areas are different, and considering their floristic diversity, the similarity value of coleopterans species between the areas is low. Marinoni and Ganho (2003, 2006); Ganho and Marinoni (2003) researched areas of Araucaria forest in the state of Paraná, and found greater similarity between the different studied areas, however the dominance of a single plant species, the araucaria, favours the similarity between insect species since the floristic richness is the same.

4. Conclusions

The abundance and diversity of insects in the "CL", an area undergoing more advanced stage of floristic restoration, are higher than the "TD", undergoing initial stage of restoration. The same pattern was verified for family richness, indicating higher values for the "CL" site compared to the "TD" site, in less advanced stage of restoration. There is

Table 2. Estimated and maximum richness, estimated and maximum diversity, evenness and similarity between the two "cordilheiras" in the Rio Negro Pantanal sub-region, Santa Emília Farm, Mato Grosso do Sul, 2005.

Parameter	Fragment	
	CL[1]	TD
Abundance	277	251
Richness (Jackknife)	33	21
Maximum richness (Jackknife)	49.5	21
Diversity (Shannon)	1.9628	1.7166
Maximum diversity (Shannon)	3.4965	3.0445
Evenness	0.5613	0.5638
Similarity	0.667	r = 0.288 ns

CL = "Cordilheira do Lau"; TD = "Cordilheira das Três Divisas"; 1/ns = non significant ($p > 0.05$).

significant difference in the coleopterofauna composition between the areas, showing a low coefficient of similarity. Therefore, the structure and the disturbance degree of the environments integrity influence coleopterofauna composition, causing the increase of abundance, richness and diversity in anthropogenic environments and those undergoing advanced stage of restoration.

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Terrestrial and aquatic mammals of the Pantanal

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(With 1 figure)

Abstract

Different works have registered the number of mammal species within the natural habitats of the Pantanal based on currently known records, with species richness ranging from 89 to 152 of annotated occurrences. Our present list sums 174 species. However, at least three factors have to be emphasised to deal with recorded numbers: 1) to establish the ecotone limit between the floodplain (which is the Pantanal) and its neighbouring domain like the Cerrado, besides the existence of maps recently produced; 2) the lack of intensive surveys, especially on small mammals, rodents and marsupials; and 3) the constant taxonomic revision on bats, rodents and marsupials. Some species are very abundant - for example the capybara *Hydrochoerus hydrochaeris* and the crab-eating fox *Cerdocyon thous*, and some are rare, and others are still intrinsically rare - for example, the bush dog *Speothos venaticus*. Abundance of species is assumed to reflect ecological resources of the habitat. Local diversity and number of individuals of wild rodents and marsupials also rely on the offering of ecological resources and behavioural specialisation to microhabitat components. A large number of species interact with the type of the vegetation of the habitat, by means of habitat selection through active patterns of ecological behaviour, resulting on dependency on arboreal and forested habitats of the Pantanal. In addition, mammals respond to seasonal shrinking-and-expansion of habitats due to flooding regime of the Pantanal. The highest number of species is observed during the dry season, when there is a considerable expansion of terrestrial habitats, mainly seasonally flooded grassland. Major threats to mammal species are the loss and alteration of habitats due to human intervention, mainly deforestation, unsustainable agricultural and cattle-ranching practices, which convert the natural vegetation into pastures. The Pantanal still harbours about a dozen of species officially listened as in danger.

Keywords: biodiversity, conservation, Pantanal habitats, mammal species, environmental threat.

Mamíferos terrestres e aquáticos do Pantanal

Resumo

Diversos trabalhos têm registrado o número de espécies de mamíferos nos diferentes hábitats naturais do Pantanal, com base nos registros do conhecimento corrente, com a riqueza de espécies variando de 89 a 152 ocorrências anotadas. Nossa lista atual soma 174 espécies. Contudo pelo menos três fatores devem ser enfatizados quando se lida com os números encontrados: 1) o limite exato do ecótono entre a bacia de inundação (que é o Pantanal) e os domínios vizinhos, como o Cerrado, apesar da existência de mapas recentes; 2) a falta de levantamentos intensivos, particularmente sobre pequenos mamíferos, roedores e marsupiais; e 3) a revisão taxonômica constante de morcegos, roedores e marsupiais. Algumas espécies são abundantes, como a capivara *Hydrochoerus hydrochaeris,* e o lobinho *Cerdocyon thous,* outras são raras e outras ainda são intrinsecamente raras, como o cachorro-vinagre *Speothos venaticus*. Assume-se que a abundância de espécies reflete os recursos ecológicos contidos nos hábitats. A diversidade local e o número de indivíduos de roedores silvestres e marsupiais também dependem da oferta ecológica de recursos e da especialização de comportamento para explorar componentes de micro-hábitats. Grande número de espécies interage com os tipos de vegetação do hábitat, por meio de seleção de hábitat com padrões ativos de comportamento ecológico, que resultam na dependência dos mamíferos de hábitats arbóreos e florestados do Pantanal. Além disso, os mamíferos respondem ao encolhimento e expansão dos hábitats devido à inundação sazonal do Pantanal, com abundância de espécies mais altas na estação seca, quando há considerável expansão de hábitats terrestres, principalmente campos inundáveis. As ameaças mais importantes para os mamíferos são a perda e alteração de hábitats devido à intervenção humana, particularmente o desmatamento, práticas de agricultura e pecuária insustentáveis, com conversão da vegetação natural em pastos. O Pantanal ainda abriga cerca de uma dúzia de espécies oficialmente ameaçadas de extinção.

Palavras-chave: biodiversidade, conservação, hábitats do Pantanal, espécies de mamíferos, ameaças ambientais.

1. Introduction

The Pantanal wetland is largely known worldwide for its extraordinary wildlife, particularly the mammal species, which include jaguar, capybara, marsh deer, giant anteater, and many others, interacting in complex ecological communities. The Pantanal is composed of different landscapes constituted of habitat gradients which offer feeding and reproductive ecological niches, sustaining a high diversity of mammal species. The high heterogeneity of the Pantanal promotes the selection of different habitats by species which widely overlap in habitat use. The Pantanal community compositions are subject to an annual hydrological cycle which determines the ecosystem functioning and the high seasonal productivity, supporting a diverse and abundant fauna, including large and endangered mammal species (Alho et al., 1988; Alho, 2005a, 2008). These factors have influenced diversity throughout life history and nowadays also influence the presence of species competing for daily needs to survive and reproduce.

Several surveys on a different time scale have shown the great magnitude of the mammalian fauna of the Pantanal: on mammalian biomass (Schaller, 1983), on occurrence of species (Alho et al., 1988; Trolle, 2003), of a literature review (Coutinho et al., 1997; Rodrigues et al., 2002), on working group results (Marinho Filho, 2007), on responses to seasonal flooding (Mamede and Alho, 2006), on microhabitat use among small mammals (Lacher and Alho, 1989), on ecology (Alho, 2005a, 2008), and studies on single species such as capybaras (Alho et al., 1989; Alho, 2003), jaguar (Soisalo and Cavalcanti, 2006; Azevedo and Murray, 2007), march deer (Schaller and Vasconcelos, 1978; Mauro et al., 1998; Mourão et al., 2000), ocelot (Trolle and Kéry, 2005), and other studies.

Pantanal land use is altering natural habitats to accommodate human needs. The landscape has been modified by human intervention, mainly deforestation, unsustainable agricultural and cattle-ranching practices, which convert the natural vegetation into pastures (Alho et al., 1988; Alho, 2005a, 2008; Harris et al., 2005). Therefore, some natural habitats are in distress. The aim of this review is to present comprehensive ecological information that forms the magnitude foundation of the mammal species diversity in the Pantanal. We check out the mammal species already reported to occur in the Pantanal, and discuss the relevant patterns of habitat use and conservation strategies. Secondarily, the purpose here is to identify new lines of research (new perspectives, initiatives, analyses and interpretations) to motivate work to elucidate complex ecological phenomena, through environmental parameters, instead of simple lists of species occurrence.

2. Methods

We synthesise the literature in order to update recent developments on occurrence of wild mammal species in the Pantanal , as well as firmly relying on our two-decade work experience in the region, to identify diversity, abundance, habitat requirements, to understand mammalian dynamics. Our study also identifies major environmental threats dealing with a conservation agenda. Joining the available information, we approach comprehensive patterns of mammalian ecology, combining habitat features and species interactions in search of unifying trends for the species, populations and communities to the drastically seasonal habitats. The relevant literature on species occurrence, community composition, population densities, habitat preference, and interspecific relations of mammals in the Pantanal was surveyed.

The reviewing of records of Pantanal mammals was based on previous revisions and additional scientific literature and technical reports (Marinho-Filho and Sazima, 1998; Wilig et al., 2000; Oliveira et al., 2002; Rodrigues et al., 2002; Camargo and Fischer, 2005; Longo et al., 2007; Marinho-Filho, 2007; Carmignotto, 2004; Cáceres et al., 2008; Aragona and Marinho-Filho, 2009; Tomás et al., 2010). Species names follow Wilson and Reeder (2005) and Reis et al. (2006); classes of extinction threats follow the International Union for Conservation of Nature (IUCN) and the Livro Vermelho da Fauna Brasileira Ameaçada de Extinção (IBAMA) of the Ministério do Meio Ambiente (Brazilian Ministry of the Environment).

3. Results and Discussion

3.1. Richness of Pantanal mammals

The total number of mammal species that occur in the Pantanal wetland has been previously reported to vary between 89 and 152 (Alho et al., 2003; Alho, 2005a; Cáceres et al., 2008; Coutinho et al., 1997; Marinho Filho, 2007; Reis et al., 2006; Sabino and Prado, 2006; Tomás et al., 2010). According to the working group designated by the Ministry of Environment (Ministério do Meio Ambiente; see Marinho Filho, 2007) there are officially 132 species of mammals in the Brazilian Pantanal. Here we update this number to 170 mammal species in the Brazilian Pantanal, and to 174 species including the Pantanal floodplain in Northeastern Paraguay (Willig et al., 2000). The increased number of species reviewed here is partially related to constant progress in taxonomic revisions, especially with the support of cytogenetics to identify new species of small mammals (wild rodents and marsupials), and to the recently increase of surveys on bats – by far the richer order of mammals in the Pantanal (Figure 1) (Camargo and Fischer, 2005; Longo et al., 2007; Santos et al., 2010). Despite several mammal species being conspicuous in the Pantanal, like capybara – a symbol of the Pantanal – most of the mammal species are not easily recorded, as they present nocturnal and twilight habits. Thus, an increase in the number of mammal species is also expected as a result of improved sampling methods. Although additional species have been found over time, another difficulty to set the right number of mammal species is the problem in determining the exact limits of the Pantanal floodplain

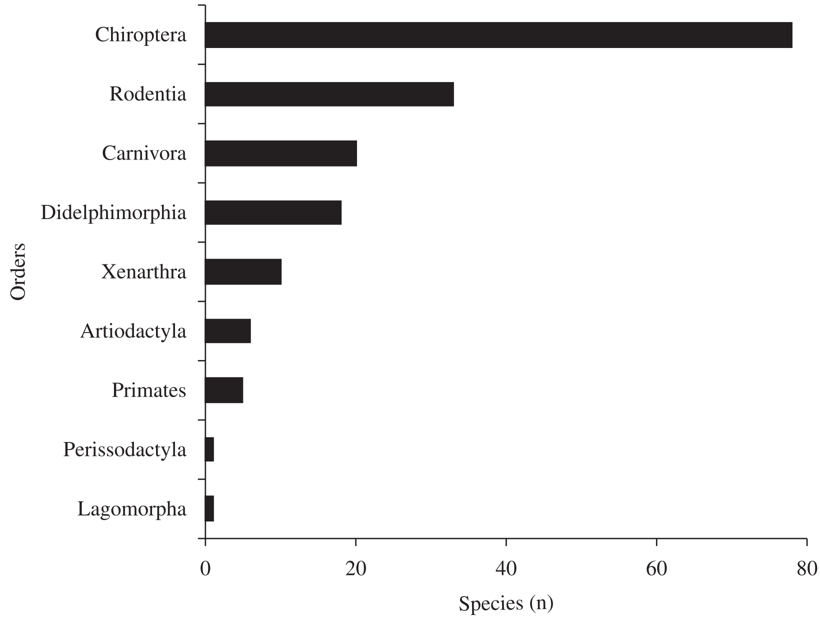

Figure 1. Species richness of nine orders of mammals which occur in the Pantanal floodplain.

relative to the surrounding domains of Cerrado, Amazonia, and Chaco.

The Pantanal is a savanna wetland (Alho, 2005a) and its biota is closer to that of Cerrado (195 mammal species), with some Amazonian and Chaco biogeographic influences. The flatland (80-150 m in altitude) has been considered the floodplain (Pantanal), and its surrounding Cerrado upland plateaus (200-1,200 m in altitude) is known as *planalto*. It helps to establish the Pantanal limits to some extent, but difficulties remain due to the complex maze of mosaic habitats, under different seasonal flooding regimes (Alho, 2008). There are official maps delimiting these bounders in the Paraguay river basin (ANA, 2004) as well as tentative delimitations of the Pantanal and its subregions based on criteria of flooding, relief, soil and vegetation type (Silva and Abdon, 1998). However, for mobile animals like wild mammals, these limits are unreasonable. Additionally, human activities have modified the landscape and so wild mammal occurrence and local distribution are changing (Alho, 2008). Unprecedented mammal species have been recorded in the uplands surrounding the Pantanal (e.g. Alho, 2000), and part of them might be expected to additionally occur in the floodplain.

3.2. Habitats and resources

The observed abundance of some species in the Pantanal habitats reveals that only a few species are common – for example the capybara *Hydrochoerus hydrochaeris*, the crab-eating fox *Cerdocyon thous*, and the flat-faced fruit-eating bat *Artibeus planirostris* – whereas some are rare or intrinsically rare – for example, the bush dog *Speothos venaticus* (Alho et al., 1988, 1989; Mamede and Alho, 2006; Alho, 2005a, 2008; Teixeira et al., 2009).

Species abundance is often assumed to be the result of availability of resources, for example, preferable habitats with a large offering of feeding and reproductive niches. This is the case of resources that affect the number of mammal species with a wide range of zoogeographical distribution like the capybara, marsh deer, crab-eating fox, but it does not apply to some species which are rare throughout all their distribution range, including the Pantanal, as is the case of the bush dog, which seems to be attached to greater ecological and behavioural specialisation, the strategy of which is to be intrinsically rare.

The patterns of habitat intergradations are even more complex in ecotone zones of broad contact between the Pantanal and Cerrado (Lacher and Alho, 2001). Habitat is an important factor in mammalian community structure. Vegetation types in different habitats influence mammal species. The physiognomic units of the Pantanal are characterised by their phytosociological and ecological arrangements, forming well-defined landscape units like seasonal flooding open fields, arboreal patches of savanna or *capões de cerrado,* semi-deciduous forest on upper grounds or *cordilheiras*, riverine and gallery forests, and others (Alho, 2005a; Silva et al., 1998). Therefore, the offering of different resources, particularly food and niches for reproduction, influences social systems of most populations of Pantanal mammals and determines local species richness, abundance, and competition.

Abundance of capybaras in the Pantanal varies seasonally, affected by changes in food abundance and available space due to annual flooding (Alho et al., 1989). Capybara's group sizes increases from the end of the rainy season to the dry season, when there are more young in the groups. During the dry season more capybaras are observed feeding on the pasture of the seasonal flooding open fields. In fact, higher densities of other mammal species occur during the dry season (August and September), when there is a considerable expansion of terrestrial habitats, mainly seasonally flooded grassland, due to the shrinking-and-expansion of habitats related to the flooding pulse (Mamede and Alho, 2006).

Capybara *Hydrochoerus hydrochaeris* and caiman *Caiman yacare* are the most common wild species killed by jaguars *Panthera onca* in the Pantanal (Azevedo and Murray, 2007), and both prey species are equally abundant in the region. Jaguars also consume a high variety of prey, including deer, peccary and others. It was estimated that the wild prey base was adequate to support the jaguar population in the study area. The study also concluded that spacing patterns in the local jaguar population were likely based on exclusion through territoriality rather than food limitation.

The total home range size area of five females and three male jaguars in the study area was 112.2 km^2 (density of 0.07 adult resident jaguars per square kilometre). Home-range size was comparable between sexes; almost half of their home range areas was shared with conspecifics of the same sex, but little overlapping was observed at the core areas, suggesting that same-sex resident individuals established exclusive core areas (Azevedo and Murray, 2007). These results indicate that prey abundance was sufficiently abundant to influence patterns of exclusivity in the spatial distribution of resident jaguars and hence prey selection patterns. Although there is indication that prey availability influences jaguar populations in the Pantanal, spatial patterns seem to be influenced by a territorial system, governed by regions of exclusivity (home range and territory), rather than by prey abundance (Azevedo and Murray, 2007).

3.3. Microhabitats and ecological resources

Local diversity and number of individuals also rely on the offering of resources and behavioural specialisation to habitat components. On a small scale, specialised species are able to exploit the spatial and temporal variation of the habitat heterogeneity, including microhabitat components (Lacher and Alho, 1989; Alho, 2005b; Carmignotto and Monfort, 2006). In the Cerrado landscape, small mammal communities differ along a gradient of natural habitats (Alho, 2005b). Community differences appear to be a function of local mosaic factors as well as differences among river basins, between high plateau forested habitats and lowland valley forests, or between moister open areas with soft soil and abundant grass versus very dry and rocky microhabitats. For example, among small mammals, like marsupials and rodents, there are habitat generalists occurring in more than three types of habitat (pan-habitat species) and habitat specialists, showing a high degree of fidelity to habitat.

It is common to find small mammal species with a preference for arboreal or forested habitats or for open habitats within the same study area. In the semi-decidous forest habitats, surrounded by open savanna habitats, woodland-dwelling genera such as *Cerradomys* and *Oligoryzomys* occur within a few metres of transition zone-habitat dwellers such as *Clyomys* and *Trichomys*. The genus *Oligoryzomys* also occur in both open and forested habitats.

Microhabitat use among small mammals in the Pantanal shows that two genera of Cicretidae rodents – *Oligoryzomys* (with two species occurring in the Pantanal: *O. chacoensis* and *O. microtis)* and *Cerradomys (C. subflavus)* – are more generalised in their use of microhabitats than are two Echimyidae species - *Clyomys laticeps* and *Trichomys pachyurus* (referred to as *T. apereoides* in some publications, but recognised as a distinct species based on chromosomal differentiation; Bonvicino and Lacher, 2008). *Oligoryzomys* species are broad habitat generalist at the "Nhecolândia" sub-region of the Pantanal. *Cerradomys subflavus* patches of arboreal savanna, *capão de cerrado*. Both *Clyomys* and *Trichomys* were restricted to their transition microhabitat. Although both genera overlap in the same microhabitat, competition is avoided since *Trichomys* is scansorial while *Clyomys* is fossorial (Lacher and Alho, 1989). In general the transition between arboreal habitats and open areas are selected by *Trichomys pachyurus* (Carmignotto, 2004).

Studies carried out in habitats surrounding the Pantanal, on plateaus of *Chapada dos Guimaraães*, state of Mato Grosso, pointed out that the combination of vegetation type and substrate structured the community of 19 terrestrial species of small mammal into several smaller communities with little faunal overlap (Lacher and Alho, 2001). This study showed that most species were captured in only one or two of the qualitative habitat types. There were open habitat species completely absent from forest, and forest species that were captured only in forest habitats. Cluster analysis of 19 species studied confirmed the separation made by qualitative classification of habitats based on plant species composition and other habitat characteristics. The results for habitat associations of small mammal species determined by cluster analysis of soil and vegetation structural characteristics (independently of plant species composition) generated five fairly distinct clusters.

The gallery forest cluster grouped the same set of species that had previously been assigned to gallery forest (*Neacomys spinosus*, *Hylaeamys megacephalus*, *Nectomys squamipes*, *Oecomys bicolor*, *Proechimys longicaudatus*, and *Caluromys philander*), confirming the earlier analysis. The cluster analysis also grouped the six species that had previously been associated with wet field (*Oligoryzomys microtis* — occurring at the Cerrado-Amazonia contact zone, *Oligoryzomys nigripes* (= *eliurus*), *Cerradomys subflavus* species group, *Necromys lasiurus*, *Monodelphis domestica*, and *Marmosa murina)*. The grouping of species was essentially the same whether it was done qualitatively by habitat type or by a quantitative analysis of structural aspects of the vegetation and substrate of the habitat (Lacher and Alho, 2001). Small mammals are more specialised regarding to habitat requirements, and so they are able to exploit different parts of the habitat mosaics of the Pantanal.

3.4. The dependence of forest habitats

The Pantanal habitats support a number of living mammal species that interact with each other and with the type of the vegetation of the habitats. How these mammal species interact with the type of the vegetation is a result of habitat selection by means of active patterns of ecological behaviour. This interaction will then determine how a given species well uses the range of habitats to fulfill its daily need for food, space, shelter, social interactions, reproduction and other living requirements, as a result of habitat selection. The local presence of these required habitat needs, like forest areas, are essential to determine population and community parameters like species richness, abundance, reproductive potential and other.

In the Pantanal there are different mammal species that rely on forest or arboreal habitats, besides are frequently observed ranging in open landscape. If this condition is met, the species will typically show populations parameters like high densities within preferable habitats. Studies on capybaras of the Pantanal show that the use of habitats varies seasonally (Alho et al., 1989; Alho, 2005a, 2008). During the dry season, capybaras spend the night in the forest. In the early morning they leave the forest to graze on the grassland. During the rainy season, the capybaras also spend the night in the forest, but in the morning usually emerge and go directly to the water or to grazing areas. Use of aquatic and forest vegetation in their diet at that time increases significantly, since few grazing areas remain above water level. Group sizes ranged from 2 to 25 individuals, depending on the kind of preferable habitats. Each group occupied an area ranging from 33.67 to 196.04 ha. Home range of a group contained foraging open area, a patch of forest (usually a gallery forest or a patch of savanna, locally known as *capão de cerrado*) and water (river, *corixo* or *baía).* The densities in the most used habitats ranged from 0.01 to 0.69 capybara/ha. Each social group occupied a core area within its home range varying from 2.97 to 52.80 ha.

Many aspects of the behaviour and ecology of the capybara are affected by seasonal fluctuations in the amount of available food. Some preferred food items that are richer in protein tend to be more seasonal than poorer food items. There is a period of the year, from June until November, when the standing crop on lower areas susceptible to flooding is abundant and is consumed by capybaras. During the remainder of the year the presence of these food items is very scarce. Thus, the times of food abundance and scarcity are predicted by the flooding pattern. Capybara group size increases from the beginning (rainy season) to the middle of the year (dry season). During the floods the groups subdivide and are largely confined to the forest patches, while in the dry season more animals are observed feeding on the pasture of the grassland (Alho et al., 1989; Alho, 2005a, 2008; Mamede and Alho, 2006).

The major part of the habitat heterogeneity observed in an ecological community of the Pantanal is determined by vegetation, mainly the arboreal or forested habitat, that comprise a matrix of high complexity, forming different strata, occupied by mammal species. In general the fauna of the Pantanal and the surrounding Cerrado present strong dependency on habitat complexity (Alho et al., 2003; Alho, 2008).

Analyses using the 15 most abundant mammal species in the Pantanal habitats (considering macroniche characteristics) have pointed out that at least ten mammal species strongly rely on the presence of arboreal or forested habitats (Alho et al., 2003). This dependence on arboreal/forest habitats can be evaluated as a function of the characteristics of the macroniche used by each mammal species, considering the body size, its requirement of habitat quality, and its type of diet and locomotion. Five species (*Alouatta caraya, Nasua nasua, Dasyprocta punctata, Cerdocyon thous* and *Mazama americana)* are dependent on arboreal/forest habitats, and so intolerant to deforestation. Five other species (*Myrmecophaga tridactyla, Ozotoceros bezoarticus, Hydrochoerus hidrochaeris* and *Tamandua tetradactyla*) have shown moderate dependence on arboreal/forest habitats. Higher abundance of forested areas in a given study area in the Pantanal seems to favour the presence of jaguars (Azevedo and Murray, 2007).

3.5. Semi-aquatic species

Mammals adapted for aquatic life in the Pantanal, with webbed feet, a dense underfur, short legs, a long body and long tail, are two carnivore species belonging to the family Mustelidae, the giant otter *Pteronura brasiliensis* and the freshwater otter *Lontra longicaudis*. The capybara is a semi-aquatic largest rodent, a keystone species of the Pantanal. Another large mammal that frequently uses habitats with presence of water is the tapir *Tapirus terrestris.* The bush dog *Speothos venaticus* has a close association with water, presenting morphological adaptation for swimming, webbed feet.

Other mammal species with some association with water are marsupials, some confined to habitats of gallery forest and other kinds of arboreal habitats with close relation to water such as rivers and *corixos*: *Marmosa murina*; *Micoureus constantiae* and *M. demerarae; Marmosops noctivagus* and *Chironectes minimus.*

Giant otter *Pteronura brasiliensis*is has a long and flattened tail, adapted for swimming. The fur is thick and glossy. They are social animals, living in groups of 5-15 related individuals. They are highly vocal and their noise is easily recognised by riverine men in the Pantanal. The social group moves according to movement of seasonal water of the Pantanal, usually following school of fishes in movement. They pursue fish and hunt in groups. The giant otter is a semi-aquatic predator which relies mainly on fish, occurring in the Pantanal in habitats with slow moving waters (rivers, *corixos* and large permanent *baías)* presenting high productivity of fish. They are diurnal mammals and form cohesive social groups, moving in function of seasonal flooding. During the dry season the social groups occupy one stretch of the river, *corixo* or *baía* and actively scent mark the occupied territory also using communal latrines.

Different surveys have shown occurrence of giant otter in the Pantanal. The species is documented to occur (active burrows with recent tracks and latrines) along 324 km of the Aquidauana river, between the town of Aquidauana and the village of Passo da Lontra, in Mato Grosso do Sul state. The greater part of this river stretch is constituted by the Aquidauana River (258 km), and the remaining 82 km correspond to the Miranda River (Tomás et al., 2000).

A study conducted at Vermelho and Miranda rivers in the Pantanal concluded that time spent by giant otters marking varied between groups (Leuchtenberger and Mourão, 2009): the alpha males marked more frequently (62% of marking events, 55 minutes) than the alpha females (17% of marking events, 13.6 minutes). The study pointed out that scent-marking among giant otter individuals within the social group can play a relevant role in communication of social and sexual status and territorial defense.

The freshwater otter *Lontra longicaudis* has a semi-aquatic habit since this species depends on the riverbanks, where they actively mark territories to rest and reproduce, and the water to search for food. Estimated density in some Pantanal areas is of one individual for each 2-3 km along the Negro river (Kruuk, 2006). They prefer clear running waters, protected by gallery forest, and river banks that can provide shelters. They prey primarily on fish, being observed alone or in small group, generally the female and its young.

3.6. Threatened species

Medium to large sized mammals (12 species), two bat and rodent species of the Pantanal are considered threatened, according to the *Livro Vermelho da Fauna Brasileira Ameaçada de Extinção* (Brazilian Red Book of the Fauna Threatened with Extinction) of the *Ministério do Meio Ambiente* (Brazilian Ministry of the Environment) based on documents published by IBAMA (*Brazilian Institute of Environment and Renewable Natural Resources – Portaria Nº. 62 in 1997*), and by the Ministry (*Instrução Normativa Nº. 3* in 2003, and *Instrução Normativa Nº. 5* in 2004) (Table 1). Among bat species are *Vampyrum spectrum* and *Chiroderma doriae*. *Phyllomys brasiliensis* is the only rodent occurring in the Pantanal redlisted as endangered in both lists (MMA, 2008a,b; IUCN, 2011). *Blastoceros dichotomus, Chrysocyon brachyurus, Leopardus pardalis, Leopardus tigrinus , Leopardus wiedii, Myrmecophaga tridactyla, Leopardus colocolo, Panthera onca, Priodontes maximus, Pteronura brasiliensis, Puma concolor,* and *Speothos venaticus* are among medium-large sized mammals listed in the Brazilian Red Book (Table 1), as well in the IUCN Redlist, which some differences in the categories (Table 1).

The marsh deer, *cervo-do-pantanal, Blastocerus dichotomus*, is the largest Brazilian deer. Interdigital membranes, extended hooves, and relatively long limbs are adaptation features to flooding habitats (Tomás et al., 1997). The threat status of this species is vulnerable, including MMA ranking as well as IUCN category. All vegetation communities in which marsh deer *Blastocerus dichotomus* have been observed (Tomás, 1993) are frequently flooded during the wet season (most habitats are formed by aquatic plants). The vegetation type most used by marsh deer is *Andropogon* grassland and other open areas are dominated by *Pontederia, Scleria, Nymphaea, Eleocharis, Thalia, Axonopus, Oryza, Nymphoides* and *Luziola* communities. Marsh deer select about 35 plant species, mainly aquatic plants. *Pontederia cordata* L. (including both flowers and leaves), *Thalia geniculata* L. (mainly flowers), *Nymphaea* spp. L., *Aeschynomene sensitiva* Sw., *A. fluminensis* Vell. Conc., *Discolobium pulchellum* Benth, *Reussia* spp. Endl., *Leersia hexandra* Sw. and others are frequently eaten by marsh deer. Tomás (1993) provides a list of those plants.

Two canid species are in danger: the maned wolf and the bush dog. The maned wolf - *lobo-guará- Chrysocyon brachyurus,* inhabits the grasslands and scrub forest of the Pantanal. It is listed as vulnerable by MMA and near threatened by IUCN. Its population is experiencing a continuing decline due to ongoing habitat loss and degradation, road kills and other threats (Rodden et al., 2008). The bush dog or *cachorro-vinagre Speothos venaticus* is categorised as vulnerable. It is an intrinsically rare species although having a wide distribution range, it is nowhere abundant and occurs at very low densities.

Bush dogs are habitat generalist, showing some preference to areas near water. Survey on direct sightings and evidences of occurrence (feces, tracks, carcasses) recorded in a protected area of the Pantanal have shown a home-range size of 150 km² occupied by a group of six bush dogs (Lima et al., 2009). It was estimated the presence of about five groups of bush dogs with sizes varying from two to five individuals, but about two was the average group size, although some isolated individuals were detected. This study identified the nine-banded armadillo *Dasypus novemcinctus* as the preferred prey of bush dogs. In forest habitats they create dens in burrows of old trees where the female nurses its young.

Threatened felid species of the Pantanal are: the ocelot or *jaguatirica, Leopardus pardalis mitis,* listed by MMA as vulnerable; the little spotted cat or *gato-do-mato-pequeno, Leopardus tigrinus,* under the threat category of vulnerable; the margay cat or *gato-maracajá, Leopardus wiedii,* listed as vulnerable; the Pampas cat or *gato-palheiro, Leopardus colocolo,* also vulnerable; the puma or *suçuarana Puma concolor* shows sympatric range with jaguar in the Pantanal (two subspecies are listed as vulnerable by MMA: *P.c. capricornensis* and *P.c.greeni*, both not occcurring in the Pantanal); and the jaguar or *onça, Panthera onca,* categorised as vulnerable. Among felid species, *Leopardus wiedii* and *Panthera onca* are categorised as vulnerable by IUCN Red List.

These species occur within the Pantanal habitats, documented in different studies. Using capture-recapture analysis, Trolle and Kéry (2005), estimated *Leopardus pardalis* density in a study area of 0.112 individuals

Table 1. List of 174 mammal species occurring in the Pantanal floodplain, ordered from the most to the least speciose groups, based on published records. Extinction threatening status by the International Union for Conservation of Nature (IUCN) and the Livro Vermelho da Fauna Brasileira Ameaçada de Extinção (MMA, 2008) is given.

ORDER **Family** **Species**	**IUCN**	**IBAMA**
CHIROPTERA		
Phyllostomidae		
Anoura caudifer (E. Geoffroy, 1818)		
Anoura geoffroyi Gray, 1838		
Artibeus cinereus (Gervais, 1856)		
Artibeus fimbriatus Gray, 1838		
Artibeus glaucus Thomas, 1893		
Artibeus lituratus (Olfers, 1818)		
Artibeus obscurus (Schinz, 1821)		
Artibeus planirostris (Spix, 1823)		
Carollia brevicauda (Schinz, 1821)		
Carollia perspicillata (Linnaeus, 1758)		
Chiroderma doriae O. Thomas, 1891		Vu
Chiroderma villosum Peters, 1860		
Chrotopterus auritus (Peters, 1856)		
Desmodus rotundus (E. Geoffroy, 1810)		
Diaemus youngi (Jentink, 1893)		
Diphylla ecaudata Spix, 1823		
Glossophaga soricina (Pallas, 1766)		
Glyphonycteris behnii (Peters, 1865) (= *Micronycteris behnii*)		
Lonchorhina aurita Tomes, 1863		
Lophostoma brasiliense Peters, 1866 (= *Tonatia brasiliense*)		
Lophostoma silvicolum d'Orbigny, 1836 (= *Tonatia silvicola*)		
*Macrophyllum macrophyllum (*Schinz, 1821)		
Micronycteris megalotis (Gray, 1842)		
Micronycteris minuta (Gervais, 1856)		
Micronycteris sanborni Simmons, 1996		
Mimon bennettii (Gray, 1838)		
Mimon crenulatum (E. Geoffroy, 1803)		
Phylloderma stenops Peters, 1865		
Phyllostomus discolor Wagner, 1843		
Phyllostomus elongatus (E. Geoffroy, 1810)		
Phyllostomus hastatus (Pallas, 1767)		
Platyrrhinus helleri (Peters, 1866)		
Platyrrhinus lineatus (E. Geoffroy, 1810)		
Pygoderma bilabiatum (Wagner, 1843)		
Sturnira lilium (E. Geoffroy, 1810)		
Tonatia bidens (Spix, 1823)		
Trachops cirrhosus (Spix, 1823)		
Uroderma bilobatum Peters, 1866		
Uroderma magnirostrum Davis, 1868		
Vampyressa pusilla (Wagner, 1843)		
Vampyrodes caraccioli (Thomas, 1889)		
Vampyrum spectrum (Linnaeus, 1758)	Nt	
Molossidae		

Table 1. Continued...

ORDER **Family** **Species**	**IUCN**	**IBAMA**
Cynomops abrasus (Temminck, 1827) (= *Molossops abrasus*)		
Cynomops planirostris (Peters, 1865) (= *Molossops planirostris*)		
Eumops auripendulus (Shaw, 1800)		
Eumops bonariensis (Peters, 1874)		
Eumops glaucinus (Wagner, 1843)		
Eumops patagonicus Thomas, 1924		
Eumops perotis (Schinz, 1821)		
Molossops temminckii (Burmeister, 1854)		
Molossus currentium (Thomas, 1901) (= *M. bondae*)		
Molossus molossus (Pallas, 1766)		
Molossus pretiosus Miller, 1902		
Molossus rufus E. Geoffroy, 1805 (= *M. ater*)		
Nyctinomops aurispinosus (Peale, 1848)		
Nyctinomops laticaudatus (E. Geoffroy, 1805)		
Nyctinomops macrotis (Gray, 1840)		
Promops centralis Thomas, 1915		
Promops nasutus (Spix, 1823)		
Vespertilionidae		
Eptesicus brasiliensis (Desmarest, 1819)		
Eptesicus furinalis (d'Orbigny, 1847)		
Histiotus velatus (I. Geoffroy, 1824)		
Lasiurus borealis (Muller, 1776)		
Lasiurus cinereus (Beauvois, 1796)		
Lasiurus ega (Gervais, 1856)		
Myotis albescens (E. Geoffroy, 1806)		
Myotis nigricans (Schinz, 1821)		
Myotis riparius Handley, 1960		
Myotis simus Thomas, 1901		
Emballonuridae		
Centronycteris maximiliani (Fischer, 1829)		
Peropteryx kappleri Peters, 1867		
Peropteryx macrotis (Wagner, 1843)		
Rhynchonycteris naso (Wied-Neuwied, 1820)		
Saccopteryx bilineata (Temminck, 1838)		
Saccopteryx leptura (Schreber, 1774)		
Mormoopidae		
Pteronotus gymnonotus Natterer, 1843		
Pteronotus parnellii (Gray, 1843)		
Pteronotus personatus (Wagner, 1843)		
Noctilionidae		
Noctilio albiventris Desmarest, 1818		
Noctilio leporinus (Linnaeus, 1758)		
RODENTIA		
Cricetidae		

Table 1. Continued...

ORDER **Family** **Species**	**IUCN**	**IBAMA**
Akodon toba Thomas, 1921		
Akodon varius Thomas, 1902		
Calomys callosus (Rengger, 1830)		
Cerradomys scotti Langguth & Bonvicino, 2002 (= *Oryzomys scotti*)		
Cerradomys subflavus (Wagner, 1842) (= *Oryzomys subflavus*)		
Holochilus brasiliensis (Desmarest, 1819)		
Holochilus sciureus Wagner, 1842		
Hylaeamys megacephalus (Fischer, 1814) (= *Oryzomys megacephalus, O. capito*)		
Kunsia tomentosus (Lichtenstein, 1830)		
Necromys lasiurus (Lund, 1841) (= *Bolomys lasiurus*)		
Nectomys squamipes (Brants, 1827)		
Oecomys bicolor (Thomas, 1860)		
Oecomys concolor (Wagner, 1845) (= *Oryzomys concolor*)		
Oecomys mamorae (Thomas, 1906)		
Oecomys roberti (Thomas, 1904)		
Oligoryzomys chacoensis (Myers & Carleton, 1981)		
Oligoryzomys fornesi (Massoia, 1973)		
Oligoryzomys microtis (Allen, 1916)		
Oligoryzomys nigripes (Olfers, 1818)		
Echimyidae		
Clyomys laticeps (Thomas, 1909)		
Phyllomys brasiliensis Lund, 1839 (= *Echimys brasiliensis*)	En	En
Proechimys longicaudatus (Rengger, 1830)		
Thrichomys apereoides (Lund, 1839)		
Thrichomys pachyurus (Wagner, 1845)		
Caviidae		
Cavia aperea Erxleben, 1777		
Galea musteloides Meyen, 1832		
Hydrochoerus hydrochaeris (Linnaeus, 1766)		
Dasyproctidae		
Dasyprocta azarae Lichtenstein, 1823		
Dasyprocta punctata Gray, 1842		
Sciuridae		
Guerlinguetus ignitus (Gray, 1867) (= *Sciurus ignitus*)		
Urosciurus spadiceus Olfers, 1818 (= *Sciurus spadiceus*)		
Cuniculidae		
Cuniculus paca (Linnaeus, 1766) (= *Agouti paca*)		
Erethizontidae		
Coendou prehensilis (Linnaeus, 1758)		
CARNIVORA		
Felidae		
Leopardus colocolo (Molina, 1782) (= *Oncifelis colocolo, L. braccatus*)	Nt	Vu
Leopardus geoffroyi (d 'Orbigny & Gervais, 1844) (= *Oncifelis geoffroyi*)	Nt	
Leopardus pardalis (Linnaeus, 1758)		Vu
Leopardus tigrinus (Schreber, 1775)	Vu	Vu

Table 1. Continued...

ORDER **Family** **Species**	**IUCN**	**IBAMA**
Leopardus wiedii (Schinz, 1821)	Nt	Vu
Panthera onca (Linnaeus, 1758)	Nt	Vu
Puma concolor (Linnaeus, 1771)		Vu
Puma yagouaroundi (E. Geoffroy, 1803) (= *Herpailurus yagouaroundi*)		
Mustelidae		
Eira barbara (Linnaeus, 1758)		
Galictis cuja (Molina, 1782)		
Galictis vittata (Schreber, 1776)		
Lontra longicaudis (Olfers, 1818)		
Pteronura brasiliensis (Gmelin, 1788)	En	Vu
Canidae		
Cerdocyon thous (Linnaeus, 1766)		
Chrysocyon brachyurus (llliger, 1815)	Nt	Vu
Lycalopex vetulus (Lund, 1842)		
Speothos venaticus (Lund, 1842)	Nt	Vu
Procyonidae		
Nasua nasua (Linnaeus, 1766)		
Procyon cancrivorus (G.[Baron] Cuvier, 1798)		
Mephitidae		
Conepatus semistriatus (Boddaert, 1785)		
DIDELPHIMORPHIA		
Didelphidae		
Caluromys lanatus (Olfers, 1818)		
Caluromys philander (Linnaeus, 1758)		
Chironectes minimus (Zimmermann, 1780)		
Cryptonanus chacoensis (Tate, 1931) (= *Gracilinanus chacoensis*)		
Didelphis albiventris Lund, 1840		
Didelphis marsupialis (Linnaeus, 1758)		
Gracilinanus agilis (Burmeister, 1854)		
Lutreolina crassicaudata (Desmarest, 1804)		
Marmosa murina (Linnaeus, 1758)		
Marmosops noctivagus (Tschudi, 1844)		
Marmosops ocellatus (Tate, 1931)		
Metachirus nudicaudatus (E. Geoffroy, 1803)		
Micoureus constantiae (Thomas, 1904)		
Micoureus demerarae (Thomas,1905)		
Monodelphis brevicaudata (Erxleben, 1777)		
Monodelphis domestica (Wagner, 1842)		
Philander opossum (Linnaeus 1758)		
Thylamys macrurus (Olfers, 1818)	Nt	
CINGULATA		
Dasypodidae		
Cabassous chacoensis Wetzel, 1980	Nt	
Cabassous tatouay (Desmarest, 1804)		
Cabassous unicinctus (Linnaeus, 1758)		
Dasypus novemcinctus Linnaeus, 1758		
Dasypus septemcinctus Linnaeus, 1758		

Table 1. Continued...

ORDER **Family** **Species**	**IUCN**	**IBAMA**
Euphractus sexcinctus (Linnaeus, 1758)		
Priodontes maximus (Kerr, 1792)	Vu	Vu
Tolypeutes matacus (Desmarest, 1804)	Nt	
ARTIODACTYLA		
Cervidae		
Blastocerus dichotomus (Illiger, 1815)	Vu	Vu
Mazama americana (Erxleben, 1777)		
Mazama gouazoubira (Fischer, 1814) (= *M. gouazoupira*)		
Ozotoceros bezoarticus (Linnaeus, 1758)	Nt	
Tayassuidae		
Pecari tajacu (Linnaeus, 1758)		
Tayassu pecari (Link, 1795)	Nt	
PRIMATES		
Cebidae		
Cebus apella (Linnaeus, 1758) (= *C. cay*)		
Mico melanurus (E. Geoffroy in Humboldt, 1812) (= *Callithrix melanura*)		
Aotidae		
Aotus azarae (Humboldt, 1811)		
Atelidae		
Alouatta caraya (Humboldt, 1812)		
Pitheciidae		
Callicebus donacophilus (d'Orbigny, 1836)		
PILOSA		
Myrmecophagidae		
Myrmecophaga tridactyla Linnaeus, 1758	Nt	Vu
Tamandua tetradactyla (Linnaeus, 1758)		
LAGOMORPHA		
Leporidae		
Sylvilagus brasiliensis (Linnaeus, 1758)		
PERISSODACTYLA		
Tapiridae		
Tapirus terrestris Linnaeus, 1758	Vu	

per km². Soisalo and Cavalcanti (2006), studying jaguars in the Pantanal, found densities ranging from 6.6 to 11.7 jaguars/100 km², depending on the survey method employed. They successfully tested the suitability of camera-trap capture-recapture sampling methods combined with telemetry technology for monitoring the status of jaguars in an open wet grassland habitat of the Pantanal. In a study area of the Pantanal, a jaguar density ranging from 6.5 to 6.7 individuals per 100 km² was estimated (Trolle and Kéry, 2005).

The giant-armadillo - *tatu-canastra- Priodontes maximus* is the largest nocturnal and fossorial living armadillo, occurring in the Pantanal. Its threatened category is vulnerable in the MMA and IUCN lists. The semi-aquatic giant otter or *ariranha, Pteronura brasiliensis,* is also categorised as vulnerable by MMA, and as endangered by IUCN (see 3.4 Semi-aquatic species).

In addition to Brazilian legislation on endangered wildlife, there are international organisations dealing with trade of wild species CITES (1979) (Convention on International Trade in Endangered Species of Flora and Fauna- *Convenção sobre o Comércio Internacional das Espécies da Flora e da Fauna Selvagens em Perigo de Extinção*) which Brazil has been a part of since 1975- Dec. nº 76.623/75; conservation and Red List or Red Data List on endangered species - IUCN (2011) (International Union for Conservention of Nature - *União Internacional para Conservação da Natureza e dos Recursos Naturais*);

knowledge, conservation and sustainable use of biodiversity (Convention on Biological Diversity - *Convenção sobre Diversidade Biológica)* (CBD, 1992) and others.

3.7. Response of mammals to seasonal flooding

Mammals respond to seasonal shrinking-and-expansion of habitats due to flooding regime of the Pantanal with highest abundance of species observed during the dry season (August and September), when there is a considerable expansion of terrestrial habitats, mainly seasonally flooded grassland (Mamede and Alho, 2006). Animal abundance (in terms of observed individual frequencies) varied during the dry and wet seasons and the seasonally flooded grassland was the most utilised habitat by mammals in the dry season.

Recurrent shallow flooding occupies 80% of the Pantanal; during the dry season flooded areas dry up. Fluctuating water levels, nutrients and wildlife form a dynamic ecosystem. A total of 36 species were observed in the field. The capybara *Hydrochoerus hydrochaeris* was the most frequent species, followed by the crab-eating-fox *Cerdocyon thous* and the marsh deer *Blastocerus dichotomus* (Mamede and Alho, 2006).

A study scanning multichannel microwave radiometres to reveal inundation patterns in the Pantanal showed maximum inundation occurring as early as February in the northern sub-regions and as late as June in the south, as a result of the delayed drainage of the region (Hamilton et al., 1996). An area of 131,000 km^2 was inundated annually during nine years of observation, between 1979 and 1987. An average area of 53,000 km^2 is inundated annually and monthly estimates of the total area inundated range from 11,000 to 110,000 km^2.

There is observed evidence that seasonal habitat availability of the Pantanal influences population parameters of mammal species. By comparing observed frequencies of animals in the survey transects, a frequency analysis was applied to check the difference of habitat utilisation by the species showed statistically significant differences among the observed habitats - seasonally flooded grassland, patches of Cerrado, gallery forest and mesophytic forest and the seasonally flooded grassland was the most utilised habitat by the species, followed by the mesophytic forest and gallery forest . Thus, there is a significant association of species utilisation and type of available seasonal habitat (Mamede and Alho, 2006). Additionally, the distribution of the marsh deer in the Pantanal varies as a function of seasonal floods (Tomás et al., 2001).

3.8. Concluding remarks: conservation implications

The terrestrial and aquatic habitats used by the Pantanal mammals have been selected over an evolutionary scale by the rhythm of annual flooding in the wet season and retraction of the water to river valleys in the dry season. Among more than 170 mammals species (see Table 1) distributed in the Pantanal's habitats, there are 14 species officially listed as in danger. In natural habitats of the Pantanal, the interacting effects of multiple ecological processes determine the health of mammalian community structure and function. If any one or more of the conditions needed for a healthy mammalian community is missing, for example, absence of an arboreal or forested area due to conversion of local vegetation into pasture, it can cause a chain reaction affecting mammalian population parameters, community structure and behavioural ecology for feeding and reproductive niches. Human activities are increasing the vulnerability of the natural habitats of the Pantanal. Changes brought about by people have caused habitat loss and alteration, more erosion and sedimentation, pollution, unusual flooding and droughts.

Large-scale habitat disturbances, such as the use of fire and the conversion of natural vegetation into pasture or soybean plantations, have the potential to alter population parameters, community structure, use of space and other ecological requirements of mammal assemblages. Patches of *cerrado* (*capões de cerrado*) and *cerradão* on *cordilheiras*, for example, are rapidly disappearing as natural vegetation is converted into agricultural land or pastures for cattle ranching. Such environmental alterations can damage mammal habitat specialists and benefit pan-habitat species, changing community composition associated with pristine habitat gradients in the Pantanal landscape.

Although the Pantanal is rich in wildlife diversity and its habitats are still in good conservation status, about 95% of its area is still privately owned, with livestock being the main economic activity. However, in addition to increasing habitat loss and alteration due to deforestation, illegal hunting, overfishing, pollution like sewage from urban areas, erosion with sedimentation of river beds, and control of jaguars related to livestock activity are significant signs of human occupation, bringing wildlife and humans into direct conflict.

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Bat-species richness in the Pantanal floodplain and its surrounding uplands

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(With 5 figures)

Abstract

We studied the bat fauna of the Pantanal floodplain and its surrounding plateaus in Mato Grosso do Sul, Brazil, based on the scientific collection at Universidade Anhanguera – Uniderp and on the *Projeto Morcegos do Pantanal* data bank at UFMS, comprising 9,037 captures of 56 species recorded from 1994 to 2007. The Pantanal surveys were carried out in the Nhecolândia, Aquidauana, Miranda, and Paraguai sub-regions; the uplands surveys took place in the Maracaju, Bodoquena, and Urucum formations. Bat specimens were mist-netted over 376 nights in 35 sites, predominantly near fruiting trees, bat shelters, and forest patches. In the floodplain 46 species were recorded (n = 6,292 individuals), and 44 species were found in the uplands (n = 2,745 individuals). Six families were recorded: Phyllostomidae (30 species), Molossidae (12 species), Verpertilionidae (nine species) Noctilionidae (two species), Emballorunidae (two species) and Mormoopidae (one species). The bat fauna was predominantly composed of insectivore (32) and frugivore (15) species. The frugivorous *Artibeus planirostris* (n = 3,101 individuals) was the commonest species in floodplain and uplands. Other common species were *Myotis nigricans* (n = 762), *Molossus molossus* (n = 692), *Noctilio albiventris* (n = 681), *Platyrrhinus lineatus* (n = 633), *Sturnira lilium* (n = 461), *Carollia perspicillata* (n = 451), *Glossophaga soricina* (n = 436), *Artibeus lituratus* (n = 320), and *Desmodus rotundus* (n = 281). In the floodplain there were three insectivores among the most common species, contrasting with the uplands dominated by the frugivores. The diversity for the 35 sites assembled (*H*' = 2.5) is comparable to that recorded for tropical forests. The bat fauna presented here represents 34% of the Brazilian bat species, and 62% of species reported for the Upper Paraguay River Basin. Additionally, five species are reported for the first time in Mato Grosso do Sul.

Keywords: bats, biodiversity, Chiroptera, habitats, Pantanal.

Riqueza de espécies de morcegos no Pantanal e no planalto em seu entorno

Resumo

Estudamos a fauna de morcegos na planície do Pantanal e nos planaltos de entorno no Mato Grosso do Sul, Brasil, com base na coleção científica da Universidade Anhanguera – Uniderp e no banco de dados do Projeto Morcegos do Pantanal, UFMS, incluindo 9.037 capturas de 56 espécies, entre 1994 e 2007. Amostragens no Pantanal foram feitas nas sub-regiões da Nhecolândia, Aquidauana, Miranda e Paraguai; no planalto as amostragens foram realizadas nas formações de Maracaju, Bodoquena e Urucum. Espécies de morcegos foram registradas ao longo de 376 noites em 35 sítios, predominantemente com o uso de redes de neblina próximas a árvores frutíferas, abrigos e florestas. Na planície, foram registradas 46 espécies (n = 6.292 indivíduos) e no planalto 44 espécies (n = 2.745 indivíduos). Seis famílias foram encontradas: Phyllostomidae (30 espécies), Molossidae (12 espécies), Verpertilionidae (nove espécies), Noctilionidae (duas espécies), Emballorunidae (duas espécies) e Mormoopidae (uma espécie). A fauna de morcegos foi predominantemente composta de espécies insetívoras (32) e frugívoras (15). O frugívoro *Artibeus planirostris* (n = 3.101) foi a espécie mais comum na planície e no planalto. Outras espécies comuns foram *Myotis nigricans* (n = 762), *Molossus molossus* (n = 692), *Noctilio albiventris* (n = 681), *Platyrrhinus lineatus* (n = 633), *Sturnira lilium* (n = 461), *Carollia perspicillata* (n = 451), *Glossophaga soricina* (n = 436), *Artibeus lituratus* (n = 320) e *Desmodus rotundus* (n = 281). Na planície, ocorreram três espécies de morcegos insetívoros dentre as espécies mais comuns, contrastando com o planalto, onde houve dominância de frugívoros. A diversidade para os 35 sítios reunidos (*H*' = 2,5) é comparável à encontrada em florestas tropicais. A fauna de morcegos apresentada aqui representa 34% das espécies brasileiras, e 62% das espécies já reportadas para a Bacia do Alto Paraguai. Adicionalmente, cinco espécies são reportadas pela primeira vez no Mato Grosso do Sul.

Palavras-chave: morcegos, biodiversidade, quirópteros, hábitats, Pantanal.

1. Introduction

Bats are often the most species-rich mammalian taxonomic group in the tropics (Patterson et al., 2001) and represent nearly one-third of Brazilian land fauna (Marinho-Filho and Sazima, 1998). Different studies have shown latitudinal gradients contributing to the understanding of geographic distribution of bat diversity, by analysis of species richness patterns on a large scale, across wide spatial areas or with regional focus (Rohde, 1992; Willig, 2000; Stevens and Willig, 2002). Another approach is to examine changes in species richness along environmental gradients, when an assemblage of interacting bat species utilizes the same resource, for example seasonal productivity, which is carried out on smaller spatial scales (Alho, 2008; Drobner et al., 1998; Wilsey and Potvin, 2000). Some environmental factors limit the occurrence and abundance of some species, including habitat heterogeneity, seasonality and conservation status (Alho, 2005; Keddy et al., 2009).

Bat communities exhibit a variety of functional groups (guilds) such as insectivores, frugivores, nectarivores, sanguivores and piscivores (Stevens and Willig, 2002). Some studies have shown these bat assemblages in different areas: trophic relations in the Phyllostomidae from Panga Reserve, southeastern Brazil (Pedro and Taddei, 1997); bat community structure in a south-east Brazilian reserve in a transition zone between Cerrado and Atlantic Forest (Falcão et al., 2003); diversity of a Cerrado habitat in central Brazil (Zortéa and Alho, 2008). Recent literature has synthesised the number of species and distribution in Brazil (Reis et al., 2007), as well as a bat community in a savanna habitat in Bolivia, near the Pantanal (Willig et al., 2000; Aguirre, 2002). Available data on bats of the Pantanal floodplain and its neighbouring uplands, particularly from Mato Grosso do Sul state, are reported in Leite et al. (1998, 2000), Taddei et al. (2000, 2001, 2003), Camargo and Fischer (2005), Gonçalves et al. (2007), Longo et al. (2007), Camargo et al. (2009), Cunha et al. (2009), and Teixeira et al. (2009).

Large and environmentally heterogeneous wetlands like the Pantanal (147,574 km² - latitude 15° 30'-22° 30' S and longitude 54° 45'-58° 30' W), exhibiting annual changes in evenness along environmental gradients, play an important role in biological diversity, because of the heterogeneity of natural habitats, offering opportunities for feeding and reproductive niches (Alho, 2008; Keddy et al., 2009). Differences in bat species abundance may respond to local environmental annual changes or to degree of habitat degradation. Because the Pantanal and its surrounding habitats harbour a large number of bat species, some common (high abundance) and some relatively rare, intensive survey efforts are needed to estimate confidently the species abundance distributions.

The aim of this study is to show the magnitude of the bat species richness and the structure of the community, evaluating relative abundance and trophic distribution within the Pantanal floodplain and throughout its surrounding Cerrado plateaus, as well as to discuss the present status of natural habitat conservation and their bat-associated species.

2. Methods

2.1. Study sites

2.1.1. Pantanal flood plain and surrounding uplands

The maze of fluctuating water levels, nutrients, and biota in the Pantanal forms a dynamic ecosystem (Alho, 2008). The degree of inundation creates a range of major habitats. Flooding occupies about 80% of the whole Pantanal. In contrast, during the dry season, most of the flooded areas stay dry, when the water returns to the river beds or evaporates. Major habitats include patches (~ 0.5-5 ha) of semi-deciduous forests (*capões*) surrounded by grasslands, belts of *cerradão* or semi-deciduous forests surrounding lagoons (*cordilheiras*), riparian semi-deciduous forests, and mono-specific forests of woody species such as *Tabebuia aurea* (*paratudal*) and *Vochysia divergens* (*cambarazal*) (Silva et al., 2000; Araújo and Sazima, 2003). The upper ground (where there are *capões* and *cordilheiras*) is at most only a couple of metres above average water level. Rivers and depressions locally known as *corixos* are lined by riparian forests. In these forest habitats, different species of *Ficus* and other trees serve as food supply and shelter for frugivores (Teixeira et al., 2009). The uplands surrounding the Pantanal are covered by senso strictu *cerrado*, *cerradão* and semi-deciduous forests, which are severely threatened by agriculture and cattle ranching (Alho, 2008; Scariot et al., 2005). Bats were sampled in 35 sites in the Pantanal floodplain and its bordering plateaus, as described below.

2.1.2. Pantanal sampling sites

Field work was carried out in 19 sites (Figure 1) in different Pantanal sub-regions and municipalities (see Silva and Abdon, 1998). In the Pantanal sub-region of *Pantanal da Nhecolândia* eight sites were sampled: Fazenda Nhumirim (18° 59' 6.93" S and 56° 37' 24.37" W), Fazenda Arara Azul (19° 23' 41.37" S and 57° 1' 43.11" W), Fazenda Guanabara (18° 14' 6.5" S and 55° 45' 0.9" W), Fazenda Campo Neta (18° 45' 38.8" S and 56° 17' 48.3" W), Fazenda Santa Terezinha (19° 22' 38.5" S and 56° 3' 20.5" W), Fazenda Baía das Pedras (19° 18' 9.78" S and 55° 47' 0.44" W), Fazenda Mangabal (19° 2' 27.91" S and 55° 49' 43.97" W), and Fazenda Barra Mansa (19° 36' 0.94" S and 56° 4' 36.31" W). In the sub-region of *Pantanal de Aquidauana* seven sites were sampled: Fazenda Conquista (19° 18' 15.54" S and 55° 14' 40.38" W), Fazenda Santa Maria (19° 19' 47.48" S and 55° 22' 50.62" W), Fazenda Olhos D'água (19° 26' 0.52" S and 55° 12' 8.71" W), Fazenda Santa Emília (19° 30' 23.24" S and 55° 36' 46.10" W), Estância Caiman (19° 57' 56'' S and 56° 18' 37'' W), Fazenda Guaicurus (20° 4' 49.96" S and 56° 28' 55.05" W), and Fazenda Santana (19° 37' 51'' S and 55° 40' 36'' W). In the sub-region of *Pantanal do Miranda* three sites were sampled: Fazenda São Bento (19° 33'

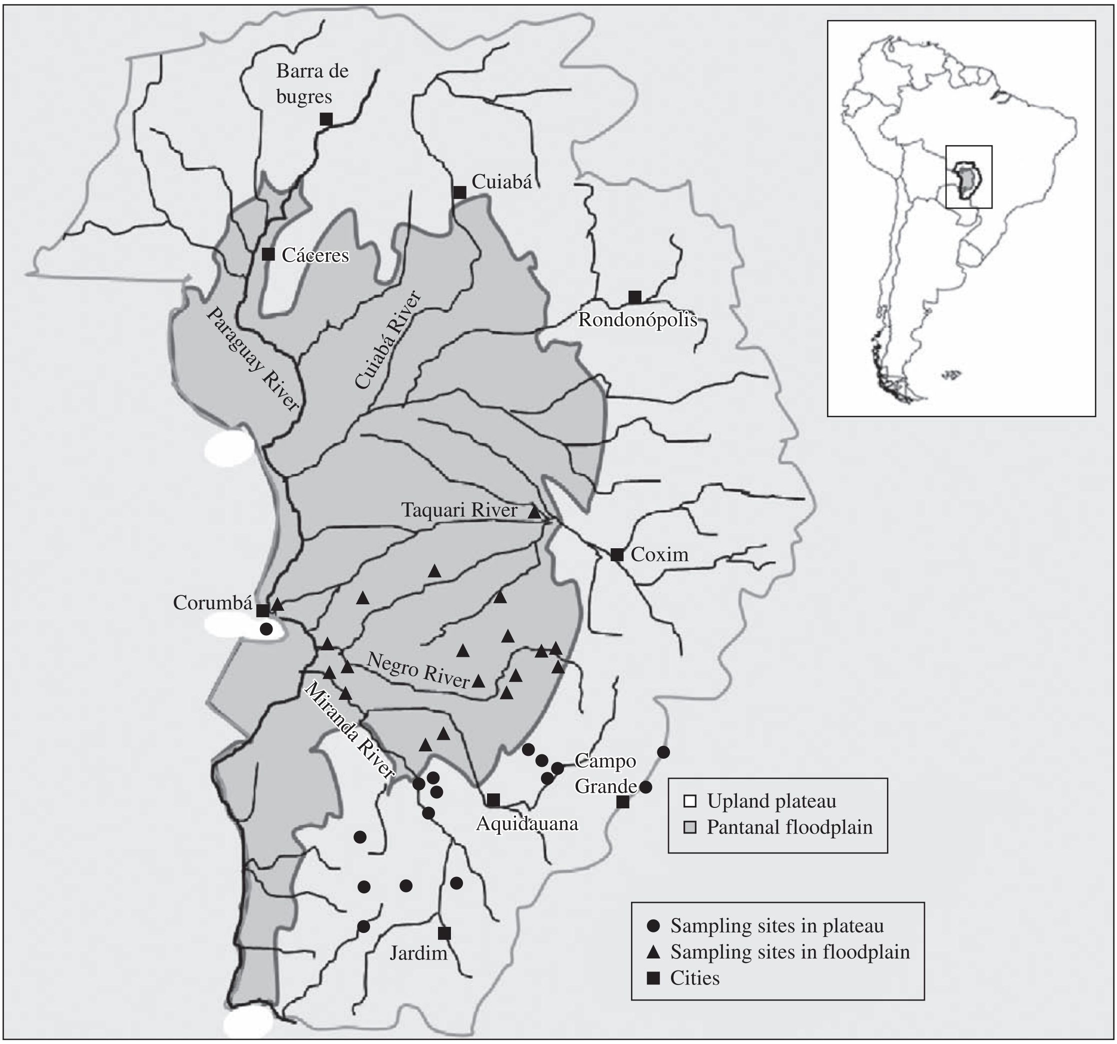

Figure 1. Sampling sites in the Pantanal floodplain (triangles) and in the neighbouring Cerrado upland plateaus (black circles), and cities (grey circles) in Mato Grosso do Sul, Brazil.

40.35" S and 57° 1' 29.44" W), Fazenda Santa Clara (19° 27' 44.10" S and 57° 4' 30.39" W), and Fazenda Sagrado (19° 25' 56.30" S and 57° 1' 40.81" W). In the sub-region of *Pantanal do Paraguai* there was one site: Fazenda Corumbá (19° 0' 35.36" S and 57° 39' 17.08" W).

2.1.3. Upland plateau sampling sites

Samplings comprised 16 sites in the plateau (Figure 1). In the Maracaju uplands there were six sites: Fazenda Furnas D'água (20° 9' 29.38" S and 55° 24' 16.02" W), Distrito de Camisão (20° 17' 11.28" S and 55° 23' 2.07" W), Distrito de Piraputanga (20° 16' 38.03" S and 55° 18' 18.54" W), Fazenda Vista Alegre (20° 5' 55.13" S and 54° 27' 26.67" W), Município de Campo Grande (20° 27' 4.58" S and 54° 36' 57.38" W), Fazenda Taboco (20° 3' 36" S and 55° 36' 20" W). In the Bodoquena uplands there were nine sites: Fazenda Campina Grande (20° 21' 22.32" S and 56° 22' 25.90" W), Fazenda Dona Benedita (20° 20' 44.78" S and 56° 26' 13.12" W), Fazenda São Cristóvão (20° 20' 16.93" S and 56° 22' 55.48" W), Fazenda São Vicente (20° 31' 25.37" S and 56° 24' 56.63" W), Fazenda Santa Tereza (21° 5' 14.27" S and 56° 3' 10.63" W), Fazenda Campo Verde (21º 24' 48.23'' S and 56º 46' 32.12'' W), Fazenda Harmonia (21° 7' 39.31" S and 56° 45' 42.04" W), Fazenda Rancho Branco (20° 41' 17.62" S and 56° 46' 42.40" W), Bonito (21° 7' 38.46" S and 56° 29' 13.68" W). In the Maciço do Urucum uplands there was one site (19° 18' 52.42" S and 57° 36' 12.19" W).

2.2. Samplings and analyses

This study relies on the bat scientific collection organised by Dr. Valdir Antônio Taddei at Universidade Anhanguera – Uniderp, Campo Grande, MS, between 1994 and 2006, with 4,239 bat specimens collected through different procedures, predominantly straightforward mist-net surveys, and on the *Projeto Morcegos do Pantanal* databank at UFMS, Campo Grande, MS, with 4,798 bat entries through mist-net captures between 1998 and 2007. Surveys covered different hydrological seasons of the Pantanal and its surroundings in different habitats, near fruiting trees, bat shelters, or forest canopies. Total capture effort was about 290,000 $h.m^2$ (time in which nets were kept open multiplied by the area of the nets), distributed throughout 376 nights, with four to 12 nets of variable sizes open per night. Biometrical data were obtained and voucher specimens were prepared for identification, which followed the criteria established by Vizotto and Taddei (1973), Taddei (1983), Anderson (1997), Lopez-González et al. (2001), Gregorin and Taddei (2002), Vicente et al. (2005), and Reis et al. (2006, 2007).

3. Results and Discussion

3.1. Bat fauna in south Pantanal and surrounding uplands

In all 35 sites 9,037 individuals belonging to 56 species, 36 genera and six families were recorded (Table 1). This number of species represents 34% of the whole richness of bats in Brazil, including the Amazon, annotated by Reis et al. (2006, 2007); it reaches 62% of the total richness reported for the entire Upper Paraguay River Basin (n = 90 bat species), including the northern area in Mato Grosso, Brazil, and the Bolivian and Paraguayan areas (Tomas et al., 2009). In the floodplain sites, 6,292 individuals of 46 species were captured, a number which reaches 64% of the bat species already registered in the whole Pantanal floodplain (Tomas et al., 2009; Alho et al., 2003); in the upland sites surrounding the Pantanal 2,745 individuals of 44 species were recorded, representing 65% of the bat species already reported to occur along the entire Pantanal borders (Tomas et al., 2009). The large number of captures and the cumulative curve of species captured (Figure 2), throughout a relatively long period of time dedicated to survey (1994-2007), indicate that overall species richness was well sampled and that this is a reliable representation of bat diversity in the focal region. In addition, five species found here – *Diphylla ecaudata*, *Mimon bennettii*, *Trachops cirrhosus*, *Uroderma magnirostrum*, and *Molossus pretiosus* – were still not reported for Mato Grosso do Sul (Cáceres et al., 2008), increasing to 66 the number of bat species registered in this state.

The richest and most abundant families in our 35 study sites were Phyllostomidae (30 species and 6,228 individuals) and Molossidae (12 species and 1,071 individuals) (Table 1), corresponding to 34% and 46% of the Brazilian species in these two families respectively (Gregorin and Taddei, 2002; Reis et al., 2006, 2007). Richness of molossid bats (all insectivorous) in the floodplain (n = 11) was almost twice that in the upland plateaus (n = 6), largely contributing to the high number of insectivorous species exclusively found in the floodplain rather than in plateaus (Figure 3). Otherwise, the number of phyllostomid species in plateaus (n = 27) was slightly higher than in the floodplain (n = 23), contributing to the increased number of exclusively frugivorous species in the plateaus (Figure 3). Although phyllostomids were richer in plateaus, the subfamily Phyllostominae presented more species in the floodplain; and it included all the insectivorous bats among phyllostomid species. Therefore, insectivory appears to be a trait which favours the occurrence of bat species in the floodplain. Indeed, even the frugivorous phyllostomids feed on insects proportionally more in the Pantanal floodplain than in its bordering plateaus or elsewhere (Munin, 2008; Teixeira et al., 2009). Diets toward insectivory might be partially explained because insects are available throughout the year, and massively during several months, whereas bat fruit sources are markedly seasonal and poor in the Pantanal floodplain (Munin, 2008; Teixeira et al., 2009).

Artibeus planirostris (n = 3,101 individuals) was by far the most dominant bat species throughout the entire focal region (Figure 4), showing one order of magnitude more captures than the next nine highly common species – *Myotis nigricans* (n = 762), *Molossus molossus* (n = 692), *Noctilio albiventris* (n = 681), *Platyrrhinus lineatus* (n = 633), *Sturnira lilium* (n = 461), *Carollia perspicillata* (n = 451), *Glossophaga soricina* (n = 436), *Artibeus lituratus* (n = 320), and *Desmodus rotundus* (n = 281). Such strong dominance of *A. planirostris* has been also reported in other local surveys in the Pantanal floodplain and in its neighbouring upland regions (Camargo, 2003; Camargo et al., 2009; Cunha et al., 2009; Teixeira et al., 2009). Although the dominance by *A. planirostris* occurred in both regions, in the Pantanal floodplain there were three insectivorous non-phyllostomid species (*Myotis nigricans*, *Noctilio albiventris*, and *Molossus molossus*) among the most common bats, contrasting with the upland plateaus where the commonest species were all frugivorous phyllostomids (Figure 4). The frugivorous *C. perspicillata* was the second most abundant species in the uplands, but it was not one of the top ten species in the floodplain (Figure 4). Thus, the relative abundance of insectivorous bats appears to be higher in the floodplain than in the uplands, probably for the same reasons which explain the exceptionally high richness of insectivores as discussed above. Calculated values for the Shannon index of diversity were similar between the Pantanal floodplain (H' = 2.3) and its neighbouring uplands (H' = 2.5). Assembling all the 35 sampling sites, diversity was found to be H' = 2.5. These values are higher than those (H' = 1.5 to 1.8) found in short-term surveys in the Bodoquena region (Camargo et al., 2009; Cunha et al., 2009), and closer to values (H' = 1.8 to 2.3) found for different areas in the Atlantic forest in southeastern Brazil (Pedro and Taddei, 1997; Esbérard, 2003).

In pockets of *cerrado* habitats the most abundant species are *Artibeus planirostris* (n = 431), *Noctilio albiventris* (n = 381) and *Molossus molossus* (n = 362). In fragments of semi-deciduous and deciduous forest on plateaus on the outskirts of the Pantanal the common species are: *Myotis nigricans* (n = 489), *Noctilio albiventris* (n = 168)

Table 1. Number of surveyed individuals from 1995 to 2007 and feeding niche of 56 bat species in the Pantanal floodplain and its surrounding upland plateaus, Mato Grosso do Sul, Brazil.

Family / Species	Number of individuals			Feeding niche
	Flood plain	Plateau	Σ	
Phyllostomidae	3856	2372	6228	
Artibeus planirostris (Spix, 1823)	2335	766	3101	Frugivore
Platyrrhinus lineatus (E. Geoffroy, 1810)	382	251	633	Frugivore
Sturnira lilium (E.Geoffroy, 1810)	199	262	461	Frugivore
Carollia perspicillata (Linnaeus, 1758)	87	364	451	Frugivore
Glossophaga soricina (Pallas, 1766)	225	211	436	Nectarivore
Artibeus lituratus (Olfers, 1818)	177	143	320	Frugivore
Desmodus rotundus (E. Geoffroy, 1810)	190	91	281	Sanguivore
Anoura geoffroyi Gray, 1838	0	124	124	Nectarivore
Lophostoma silvicolum d'Orbigny, 1836	84	13	97	Insectivore
Phyllostomus hastatus (Pallas, 1767)	59	30	89	Frugivore
Anoura caudifer (E. Geoffroy, 1818)	1	57	58	Nectarivore
Phyllostomus discolor Wagner, 1843	39	7	46	Frugivore
Chrotopterus auritus (Peters, 1856)	21	12	33	Carnivore
Platyrrhinus helleri (Peters, 1866)	8	10	18	Frugivore
Diaemus youngi (Jentink, 1893)	16	0	16	Sanguivore
Lophostoma brasiliense Peters, 1866	9	2	11	Insectivore
Mimon bennettii (Gray, 1838)	7	4	11	Insectivore
Vampyressa pusilla (Wagner, 1843)	2	5	7	Frugivore
Chiroderma villosum Peters, 1860	5	1	6	Frugivore
Chiroderma doriae Thomas, 1891	2	3	5	Frugivore
Mimon crenulatum (E. Geoffroy, 1810)	5	0	5	Insectivore
Tonatia bidens (Spix, 1823)	1	4	5	Insectivore
Micronycteris minuta (Gervais, 1856)	1	3	4	Insectivore
Phylloderma stenops Peters, 1865	0	3	3	Frugivore
Uroderma magnirostrum Davis, 1868	0	2	2	Frugivore
Diphylla ecaudata Spix, 1823	0	1	1	Sanguivore
Macrophyllum macrophyllum Schinz, 1821	0	1	1	Insectivore
Pygoderma bilabiatum (Wagner, 1843)	0	1	1	Frugivore
Trachops cirrhosus (Spix, 1823)	0	1	1	Carnivore
Vampyrodes caraccioli (Thomas, 1889)	1	0	1	Frugivore
Molossidae	833	238	1071	
Molossus molossus (Pallas, 1766)	602	90	692	Insectivore
Molossus rufus E.Geoffroy Saint-Hilaire, 1805	4	84	88	Insectivore
Molossops temminckii (Burmeister, 1854)	50	21	71	Insectivore
Cynomops abrasus (Temminck, 1827)	42	0	42	Insectivore
Eumops auripendulus (Shaw, 1800)	34	6	40	Insectivore
Molossus pretiosus Miller, 1902	39	0	39	Insectivore
Nyctinomops macrotis (Gray, 1840)	0	28	28	Insectivore
Promops centralis Thomas, 1915	26	0	26	Insectivore
Cynomops planirostris (Peters, 1865)	21	0	21	Insectivore
Eumops glaucinus (Wagner, 1843)	11	0	11	Insectivore
Nyctinomops laticaudatus (E.Geoffroy Saint-Hilaire, 1805	1	9	10	Insectivore
Promops nasutus (Spix, 1823)	3	0	3	Insectivore

Table 1. Continued...

Family / Species	Number of individuals			Feeding niche
	Flood plain	Plateau	Σ	
Vespertilionidae	895	92	987	
Myotis nigricans (Schinz, 1821)	712	50	762	Insectivore
Myotis albescens (E. Geoffroy, 1906)	109	7	116	Insectivore
Eptesicus furinalis (d'Orbigny and Gervais, 1847)	15	21	36	Insectivore
Lasiurus ega (Gervais, 1856)	22	1	23	Insectivore
Myotis riparius Handley, 1960	15	4	19	Insectivore
Myotis simus (Thomas, 1901)	18	0	18	Insectivore
Lasiurus blossevillii (Lesson and Garnot, 1826)	0	7	7	Insectivore
Eptesicus brasiliensis (Desmarest, 1819)	3	1	4	Insectivore
Lasiurus cinereus (Beauvois, 1796)	1	1	2	Insectivore
Noctilionidae	690	41	731	
Noctilio albiventris Desmarest, 1818	641	40	681	Insectivore
Noctilio leporinus (Linnaeus, 1758)	49	1	50	Piscivore
Emballonuridae	18	0	18	
Rynchonycteris naso (Wied-Neuwied, 1820)	13	0	13	Insectivore
Peropteryx macrotis (Wagner, 1843)	5	0	5	Insectivore
Mormoopidae	0	2	2	
Pteronotus parnellii (Gray, 1843)	0	2	2	Insectivore
Σ	6292	2745	9037	

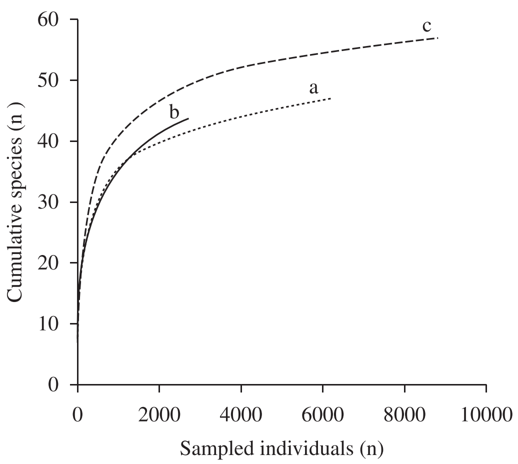

Figure 2. Rarefaction curves for bats sampled in 19 sites in the Pantanal floodplain (a), and in 16 sites in the surrounding upland plateaus (b), in Mato Grosso do Sul, Brazil. The upper curve refers to all these 35 sites assembled (c).

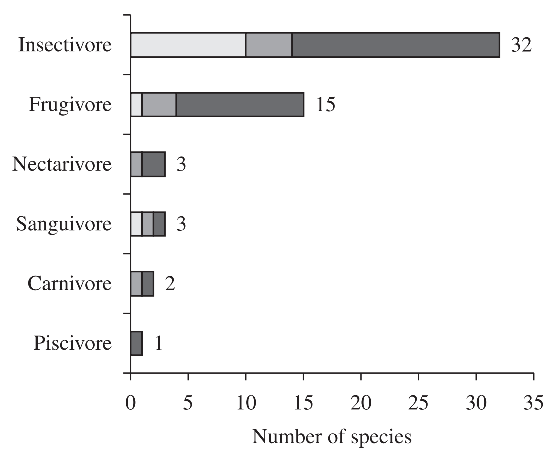

Figure 3. Richness of bats according to feeding niche, based on 9,037 individuals examined belonging to 56 species, in the Pantanal floodplain and in its neighbouring upland plateaus, Mato Grosso do Sul, Brazil. Light grey bars indicate species exclusive to the floodplain, grey bars species only found in plateau, and dark grey bars those occurring in both floodplain and plateau.

and *Molossus molossus* (n = 155). In disturbed areas, near the houses of cattle ranchers, the common species are: *Carollia perspicillata* (n = 129), *Molossus molossus* (n = 125) and *Artibeus planirostris* (n = 97). Figure 5 shows the distribution of the species within three major kinds of habitats: *Cerrado*, disturbed habitats and semi-deciduous forest of plateaus. On the other hand, 24 rare species were detected, such as *Chiroderma doriae, Chrotopterus auritus*, and *Artibeus lituratus* (Table 1). *Chiroderma doriae* is a species which requires habitat integrity and so

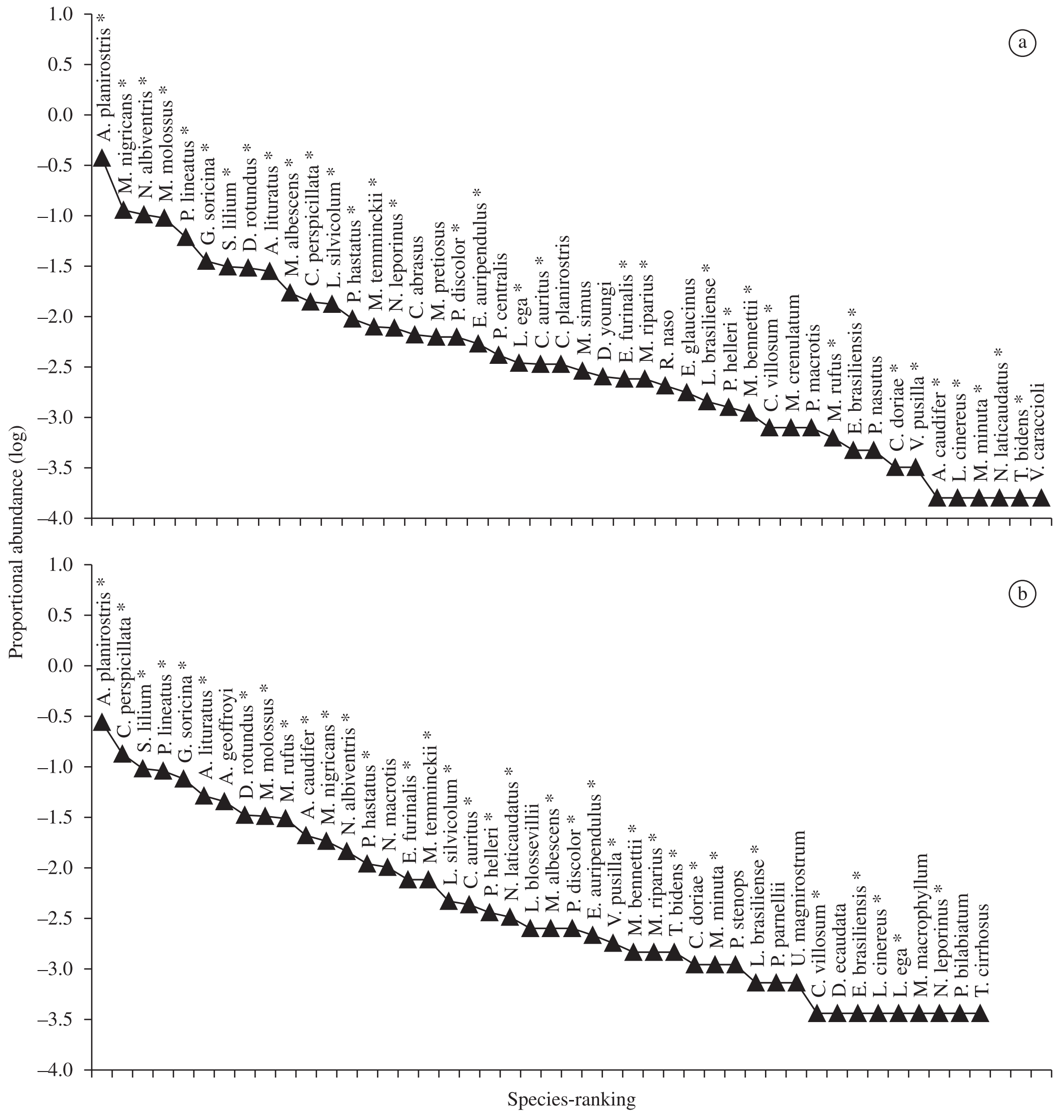

Figure 4. Rank abundance distribution of 56 species of bats in a) the Pantanal floodplain and b) its surrounding upland plateaus in Mato Grosso do Sul, Brazil. Asterisks indicate species which were recorded in both the floodplain and uplands.

is sensitive to disturbance. Some authors (Bergallo et al., 2000) consider this species as threatened by extinction, but it is not listed in the "Livro Vermelho da Fauna Brasileira Ameaçada de Extinção [The Red Book of Brazilian Fauna under Threat of Extinction]", published by the Ministry for the Environment (Ministério do Meio Ambiente) in 2008. No species found in our survey for the Pantanal is officially listed as threatened. *Chrotopterus auritus* is a large carnivore/insectivore, preying on small mammals, birds and insects, which is very sensitive to environmental disturbance, requiring good forest habitats and shelter in caves. *Artibeus lituratus* was recorded at only 1.5% in our study, but it is a good coloniser of disturbed habitat, besides living in low densities. The survey conducted in the region of Aporé-Sucuriú, northern Mato Grosso do Sul, revealed that the most caught family was Phyllostomidae, represented by *Glossophaga soricina* and *Artibeus lituratus;* and some rare species such as *Lophostoma brasiliense*, *Lonchophylla mordax* and *Lionycteris spurrelli* (Bordignon, 2006).

To analyse possible grouping of species or assemblages in the three major habitats, we performed a non-metric multi-dimensional scaling analysis taking the frequencies of species distribution, and found that the grouping composed of *Myotis albescens, Molossops temminckii, Sturnira lilium, Phyllostomus hastatus, Desmodus rotundus, Glossophaga soricina, Carollia perspicillata, Platyrrhinus lineatus, Molossus molossus, Artibeus planirostris* and *Noctilio albiventris* occurs in the three major habitats: *cerrado*, semi-deciduous forest and disturbed habitats (with 82% of similarity).

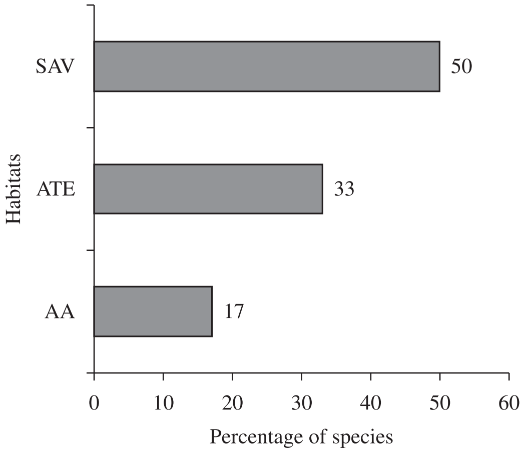

Figure 5. Distribution of the bat species in three major habitats in Mato Grosso do Sul, Brazil. SAV: savanna or Cerrado; AA: disturbed areas near ranches and other human occupation; and ATE: the ecotone zone between the floodplain and the upland "planalto", covered by semi-deciduous forest.

3.2. Bat species as bio-indicator

The Pantanal is undoubtedly an important domain and therefore deserves comprehensive ecosystem studies. Our present information on bat species richness and assemblages, considering such abundant sampling data, contributes to making a more general interpretation of species magnitude for conservation purposes. Bat species, for example, can serve as indicators for habitat quality. Natural habitats of the Pantanal have been disrupted by non-sustainable practices of socio-economic development, mainly by conversion of natural vegetation to pastures for cattle ranching and agriculture (Alho, 2008). Farms have been established in the floodplain and in its surrounding uplands, where much of the natural vegetation has been converted to soybean plantations or to other human activities. Studies concluded that 17% of the Pantanal has been deforested through the use of fire (mainly *cerrado* patches or "*capões de cerrado*"), with an annual rate of deforestation of 2.3%; and 63% of the natural vegetation cover of the surrounding plateaus in the Planalto (savanna woodland and semi-deciduous forests) has been destroyed (Harris et al., 2005). Deforestation between1976 and 2008 in the Pantanal floodplain increased 26.5 times (12.14%), compared to 40.97% of deforestation within the Upper Paraguay basin (Silva et al., 2010).

In pastures continuously used for cattle ranching, the dominance of *A. planirostris* in the bat assemblages is higher than in areas used intermittently by cattle (C. Santos, unpublished data), indicating that cattle ranching may cause a reduction in bat diversity. In addition, fire events seem to promote changes in bat species composition. *Artibeus planirostris* has been found to be the most abundant bat in both burned and unburned sites in the floodplain; however, after fire, the insectivorous phyllostomine bats increase in abundance, whereas the abundance of frugivorous stenodermatines and nectarivorous glossophagines decreases (C. Santos, unpublished data).

Our data show a high number of Phyllostomidae, which may represent a good indicator for low levels of habitat disturbance (Pedro at al., 1995; Pedro, 1998; Medellín et al., 2000). This family is well diversified in number of species and in feeding habits. The high number of frugivore species in the family implies that the habitats support a high number of fruit-bearing trees (see Pott and Pott, 1994). In addition, the high primary production favours an increased abundance of arthropods, which supports the guild of insectivore bats. The abundance of frugivore species reflects the importance of this guild for the Pantanal bat assemblages. In addition, bats play an important role in regulating the Pantanal ecosystem as seed dispersers, pollinators and regulators of insect populations (Gonçalves et al., 2007; Munin, 2008; Teixeira et al., 2009). Given that some bat species or bat assemblages require pristine habitat conditions while others are opportunistic, taking advantage of some disturbance, the group should be more studied as an indicator of levels of change in the natural environment. Drastic human alteration in natural habitats may result in simplifying bat diversity and assemblage, since those species which require more specific items in feeding strategy tend to disappear, while those with a wide spectrum of feeding habits, such as insectivore-omnivore and frugivore-omnivore, are generally less affected by environmental changes.

Effects of forest fragmentation on frugivore and nectarivore species have been pointed out in French Guiana (Cossons, 1999). The role of frugivorous bats has been emphasised in tropical forest succession (Muscarella and Flemming, 2007). Overall, Phyllostomid bats have been identified as indicators of habitat disruption in the Neotropics (Fenton et al., 1992). Work conducted in forest habitats of Paraguay has shown that abundance was highest for *Artibeus lituratus* in deforested landscapes and for *Chrotopterus auritus* in forested habitats; in contrast, *Artibeus fimbriatus*, *Carollia perspicillata*, *Glossophaga soricina*, *Platyrrhinus lineatus*, *Pygoderma bilabiatum*, and *Sturnira lilium* attained highest abundance in moderately fragmented forest landscapes. Forest cover, patch size, and patch density frequently were associated with abundance of species (Gorresen and Willig, 2004).

Therefore, our data indicate that bat species richness and assemblages in the Pantanal and its surrounding habitats are still well preserved, and it is hoped that these findings may be useful for constructive lines of biodiversity conservation and management in this important wetland ecosystem.

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Introduced species in the Pantanal: implications for conservation

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Abstract

Land use and human occupation within the natural habitats of the Pantanal have facilitated introduction of invasive species of plants and animals, including domestic species. Exotic species threaten regional biodiversity because they modify ecological community structure, alter natural habitats and affect local biodiversity. An international organisation, the International Union for Conservation of Nature (IUCN), and the Brazilian government, identify invasive species as the third most important threat to biodiversity, following habitat loss and direct effect on species. In addition, exotic species carry pathogens or may function as vectors or reservoirs for diseases that affect regional biota.

Keywords: biodiversity, exotic species, invasive species, introduced species, Pantanal.

Espécies introduzidas no Pantanal: implicações para conservação

Resumo

O uso da terra e a ocupação humana nos hábitats naturais do Pantanal têm facilitado a introdução de espécies invasivas de plantas e animais, incluindo espécies domésticas. As espécies exóticas ameaçam a biodiversidade regional porque modificam a estrutura das comunidades ecológicas, alteram hábitats e afetam a biodiversidade. A organização internacional União Internacional para a Conservação da Natureza (IUCN) e o Governo brasileiro identificam as espécies invasoras como a terceira maior ameaça para a biodiversidade, seguida da perda de hábitat e do efeito direto sobre espécies. Além disso, espécies exóticas são portadoras de patógenos ou podem funcionar como vetores ou reservatórios de doenças que afetam a biota.

Palavras-chave: biodiversidade, espécies exóticas, espécies invasivas, espécies introduzidas, Pantanal.

1. Introduction

Following human occupation, there have been introductions of exotic plants and animals, in a deliberate or accidental manner, with consequent alterations of the natural ecological communities within the Pantanal. An introduced species is one which occurs outside its geographical distributional range, being an alien, exotic, non-indigenous, invasive or non-native species. These species threaten biodiversity because they modify the community structure, changing the habitat and displacing native species.

The Brazilian Ministry for the Environment (Ministério do Meio Ambiente - MMA) considers introduced species the second greatest cause of species extinction, affecting biodiversity (Coradin, 2006). The Convention on Biological Diversity, signed by Brazil, in its Article 8 (h) establishes that each country that is party to the Convention has to make efforts to control or eradicate exotic species. The MMA publication on the subject mentions 176 exotic species occurring within terrestrial environments in Brazil, including 68 invasive animal species and 108 species of flora. Additionally, 49 invasive species were identified for aquatic ecosystems of Brazilian continental waters, including one microorganism, one crustacean, six aquatic macrophytes, four mollusks and 37 species of fish. Exotic species found within the productive fields (crops, ranches and farms) were 155 species, including bacteria, fungus, insects and other arthropods.

A global population of 6 billion people and rapid means of transport increase the spread of invasive species. For example, the vector for dengue in Brazil is the mosquito *Aedes* *aegypti* (Linnaeus, 1762), which came from Africa, probably from the Ethiopian region, brought with slave-trafficking ships in the 16th to 19th centuries. Another introduced species is *Aedes albopictus* (Skuse, 1895), which came to Brazil in 1986 and can be the vector for yellow fever (Segura et al., 2003; Walker 2007).

The International Union for Conservation of Nature (IUCN) created the Invasive Species Specialist Group (ISSG) as a global network of scientific and policy experts to deal with introduced species. They indicate that invasive species are the third most severe threat to wild mammals after habitat loss and utilisation such as hunting for food; invasive species are also the third most severe threat to birds; the fourth cause of death among reptiles (after pollution persecution and natural disasters); and the fifth most severe threat to Amphibians (following habitat loss, pollution, diseases and fires). The IUCN maintains a database named Global Invasive Database (http://www.issg.org/database/welcome/).

The introduction of species may be intentional or involuntary, but it is always related to human action and always results in environmental disruption (Fine, 2002). The negative effects include predation, competition, consequences of wild fire (since introduced species may recover better after a fire), and many other processes which lead to displacement of native species and alteration of natural ecological communities (Alho and Gonçalves, 2005; Alho, 2005, 2008; McGeoch et al., 2010).

The aim of this review article is to evaluate the present role of invasive exotic species within the Pantanal habitats, based on existing published knowledge, to discuss their possible effects on ecological communities and to consider the consequences of this threat on conservation objectives.

2. Results and Discussion

The Pantanal and its surrounding upland plateau have experienced the introduction of alien species such as the African grass *Brachiaria* (Griseb) spp., the feral hog *Sus scrofa* (Linnaeus, 1758), locally known as "porco monteiro", and recently the golden mussel *Limnoperna fortunei* (Dunker, 1857), locally known as "mexilhão-dourado", accidentally brought from China. The Amazonian fish "tucunaré" *Cichla cf. ocellaris* Bloch & Schneider 1801, a voracious predator introduced in the Pantanal, has already impacted the regional fish community. Herbivores like cattle and water buffalo can wreak great damage, since they require introduced pastures and exert pressure on native plant species.

The domestic animals introduced, with effects on natural systems, include cattle, horses, dogs, cats, chickens and many others, all from direct human action. Alien species in the Pantanal have caused alterations in the life history of native plants as well as of wild animals.

2.1. Introduced plants

Natural pastures of the Pantanal are mainly formed by species such as *Axonopus purpusii* (Mez) Chase, *Mesosetum loliiforme* (Hochst. ex Steud.) and *Panicum laxum* Sw., covering the open fields and sandy soils of the floodplain. Other plant species forming homogeneous fields are present, such as the legume *Desmodium barbatum* (L.) Benth and the *fura-bucho* belonging to the genus *Paspalum* (Santos et al., 2006). Since these natural pasture fields remain submerged during the wet season, cattle ranchers are introducing exotic grassland species on the higher grounds of the Pantanal. Cultivated pastures have been expanding rapidly in the floodplain to compete with the ranchers located in the upper Cerrado plateaus surrounding the Pantanal. Two exotic species dominate the pastures: *Brachiaria decumbens* Stapf and *Brachiaria humidicola* (Rendle)Schweick. These two exotic species aggressively cover the ground and have been widely used to convert natural vegetation into cultivated pastures.

Grasses are among the invasive species with a high capacity to colonise woodland, such as denser areas of *Cerrado* that is being converted into open fields. In the case of *B. decumbens,* its capacity to exclude native species has been pointed out (Matos and Pivello, 2009; Oliveira, 2004). On the plateaus surrounding the Pantanal, grass species such as *B. decubens* and *capim-gordura Melinis minutiflora* Beauv. are great challenges for control in protected areas. This is also the case of Emas National Park (Parque Nacional de Emas) in the state of Goiás, east of the Pantanal. It has been shown that *B. decumbens* is the species that most benefits from wild fire, common in the region during the dry season.

There are some local plant species of the Pantanal which take advantage of disturbed areas and grow aggressively, dominating and modifying natural habitats. Species locally known as *assa-peixe* (*Vernonia scraba* Pers. and *Vernonia ferruginea* Less.), can colonise areas along open routes or roads. Other species which benefit from altered habitats, proliferating abnormally, are *Bromelia balansae* Mez. and *Byrsonima intermedia* A.Juss, *B. orgignyana* A. Juss and *Licania parvifolia* Huber. The bush locally known as *pombeiros,* belonging to the genus *Combretum,* can form homogeneous plots known as *pombeiral* after certain types of disturbance and abnormal flooding. The same trend is observed with the proliferation of the *cambará* (*Vochysia divergens* Pohl.), forming homogeneous *cambarazais*; and the dominance of *lixeira* (*Curatella americana* L.) forming *lixeirais* (Santos et al., 2006).

2.2. Livestock

Cattle-ranching is an important economic activity within the Pantanal. The introduction of water buffalo (*Bubalus bubalis* Linnaeus, 1758) is relatively recent. It is estimated that there are more than 5000 head of buffalo in the region (Mourão et al., 2002).

In addition to the conversion of natural vegetation into introduced cultivated pastures, the intensely herbivorous diet of cattle alters vegetation cover, modifying community structure. The evidence of the effects of large domestic herbivores, such as cattle and water buffalo, grazing on vegetation may be seen in recently protected areas where cattle used to be established: the open areas immediately recover in structure and function. Herbaceous phytomass is consumed under different grazing strategies by cattle and water buffalo, which are distinguished by their effects on herbaceous productivity. There are direct effects on plant productivity and survival; besides constant loss of biomass to herbivores, grazing usually results in the introduction of exotic species. Large domestic herbivores affect vegetation, both directly by consuming a large portion of its biomass and also indirectly by being selective in preferred items, compacting the soil, foraging on woody vegetation (browsing) and dispersing seed-propagating species, such as the *acuri* palm tree *Attalea phalerata* Mart. ex Spreng.

2.3. Feral pig

The feral pig, known in the Pantanal as *porco-monteiro,* escaped from domestic herds and became wild. These animals form groups, then damaging crops, digging up large areas of native vegetation, particularly near the depressions with temporary or permanent water known as *baías,* and may transmit disease to wildlife. It has been estimated that there are nearly 10,000 groups of *porco-monteiro* in the Pantanal (Mourão et al., 2002). It is more abundant in the sub-region of Aquidauana and within the regions with less flooding, such as Nhecolândia and Paiaguás. A study carried out in the Pantanal of Rio Negro, between April 2003 and March 2004, showed that the *porco-monteiro* was the second most abundant mammal in the survey, second only to capybara *Hydrochoerus hydrochaeris* Linnaeus, 1766 (Mamede, 2004). Seasonally flooded habitats are preferred by the animals, which particularly forage in sites near temporary *baías.*

The *porco-monteiro* has rapidly adapted to the environmental conditions of the Pantanal, with morpho-physiological and behavioural characteristics that resemble its original wild ancestors more than the domestic pig. They are omnivorous and can occasionally prey upon young animals. They also take eggs and all kinds of soil invertebrates and vertebrate species they are able to capture. Local residents hunt juveniles for food. Some of the young males are captured, castrated and released to be caught again, when older, for food.

Feral pigs probably occupy the same habitat requirements that local white-lipped peccary or *queixada* (*Tayassu peccary* Link, 1795) and collared peccary *cateto (Pecari tajaco* Linnaeus, 1758*)* do, particularly in terms of feeding strategies (Sicuro and Oliveira, 2002). Niche partitioning among sympatric populations of white-lipped peccary, collared peccary, and feral hog was evaluated using an ecomorphological approach: morphofunctional data suggest that feral hogs have a powerful bite and are able to feed on seeds of different degrees of resistance (Sicuro and Oliveira, 2002). This study indicates that with an optimised lever system of head elevation, feral pigs are more efficient than peccaries at rooting. In addition, feral hogs explore a wide range of habitats, which supports the view that the invasive species acts as a potential competitor of native peccaries. However, overlaps in food resources and habitat use between feral pigs and peccaries in the Pantanal were found to be lower than expected (Desbiez et al. 2009). In fact, this study shows that niche overlap was highest between the native species. Differences in morphology and behaviour indicate possible mechanisms of niche partitioning between the species.

2.4. African bees

The African bee *Apis mellifera scutellata* (Lepeletier 1836) was introduced into Brazil in 1956 and has spread throughout the country and others in the region. The so-called 'africanized bee' or *abelha africanizada* is a hybrid of the European bee *Appis mellifera mellifera* Linnaeus, 1758. It has adapted very well to the environmental conditions of the biome and exhibits aggressive behaviour, attacking humans and animals, such as horses, in the Pantanal.

2.5. Introduced fishes

The *tucunaré* is believed to have been introduced in the region in the 80's. It is thought that the introduction occurred in 1982, when a water reservoir for raising *tucunaré* broke, releasing the fishes into the Itiquira and Piquiri rivers, on the border of the states of Mato Grosso and Mato Grosso do Sul (Ferraz de Lima, 1993). Surveys carried out indicate that *tucunarés* were confined to the Piquiri river basin between 1992 and 1994 (Nascimento et al., 2001). However, over the following years, the fish has been reported occurring in other river basins of the Pantanal, including in several localities along the left bank of the Paraguay river, São Lourenço River and Paraguay-Mirim River, (Marques and Resende, 2005). The *tucunaré* does not migrate for reproduction and prefers clear and non-turbulent water.

This large fish is a voracious Amazonian carnivore preying upon native species, competing for food and space with local species, disrupting ecological fish communities in a cascading scale in the trophic food chain (Harris et al., 2005). However, there are no regional studies on the real role of *tucunaré* in the Pantanal aquatic habitats.

Another fish species recorded in the Pantanal is the Amazonian *tambaqui* (*Colossoma macropomum* Cuvier, 1816*)* whose biology resembles the natural history of the local *pacu* (*Piaractus mesopotamicus* Holmberg, 1887)*,* both feed largely on fallen fruits and seeds.

2.6. Introduced mollusk

The bivalve mollusk *Limnoperna fortunei* (Dunker, 1857*),* known as *mexilhão-dourado,* was introduced into the Paraná-Paraguay rivers and has reached the Pantanal. It arrived in Argentina's River Plate in 1991, brought by ships from China (Darrigan and Pastorino, 1995, 2003; Oliveira et al., 2000). Ships arriving from Asia had discharged ballast water containing the mussels or their larvae into the Plate. From this river, the molluscs reached the Paraná-Paraguay rivers, giving them access to the vast Pantanal wetland.

It has been reported to occur in the Paraguay River since 1998, up to the region of Bela Vista do Norte, near the tributary of the Cuiabá River, in several lakes or *baías* adjacent to the Paraguay River; and later on, in 2003, it was also reported in the Miranda river, near the region of Passo do Lontra (Oliveira, 2003).

It also occurs at the bottom of a lake (Baía do Tuiuiú -18º 49' 18" S and 57º 39' 13" W), near Corumbá city. In 1999 it was registered in the Paraguay River (17º 38' 04" S and 57º 41' 45" W), near Forte Coimbra, encrusted on rocks. However, a study carried out by Oliveira (2003) points out that the densities of *mexilhão-dourado* in the Paraguay river (10,000 individuals/ m²) are lower than the densities found in aquatic habitats in southern Brazil (100,000 individuals/ m²).

Another introduced mollusk is the African snail *Achatina fulica* Bowdich, 1822, which arrived in Brazil around 1980, brought to substitute the escargot *Helix aspersa* Müller, 1774 as a delicacy (Carvalho Jr. and Nunes, 2009). *Achatina fulica* is partially an arboreal and herbivore generalist species and was introduced into the Pantanal as bait brought by fishermen. This African mollusk is currently found throughout the Pantanal (Carvalho Jr. and Nunes, 2009; Instituto Horus, 2009; Teles et al., 1997).

The North-American frog *Rana catesbeiana* Shaw, 1802 = *Lithobates catesbeianus* (Shaw, 1802) was introduced into Brazil to be raised as a food source; it accidentally escaped and is now found in several different regions. There is no official record of this species in the Pantanal, but some people claim to have heard its call.

2.7. Dogs, cats, rats, mice and others

Domestic or pest mammal species introduced by man into the Pantanal, including the domestic dog *Canis familiaris* Linnaeus, 1758, cat *Felis catus* Linnaeus, 1775, mouse *Mus musculus* (Linneaus, 1758) and black rat *Rattus rattus* (Linnaeus, 1758), are potential predators of wildlife and infest ecological ecosystems, spreading diseases and causing habitat degradation. Cats are known to prey on birds' nests and on lizards, amphibians and other small animals. Dogs are trained to hunt wildlife. In some protected areas feral dogs may impact biodiversity. The effect of these alien invasive species may be viewed as the simple and direct effect of one given introduced species on any natural ecosystem. However, in a more complex analysis, considering a greater number of variables that can be identified and derived from invasive species, domestic mammals and others can be examined simultaneously interacting among themselves as well as with the native species. The result is generally the impoverishment of local biodiversity. These species may also carry diseases that affect wildlife and man: dogs, for example, harbour the pathogen of leishmaniasis.

2.8. Concluding remarks

From the introduced species reviewed here, the adverse effect of invasive species on biodiversity and natural habitats of the Pantanal is evident. Some alterations in community structure and function have been rapid and highly noticeable, while others are slow but ongoing; both trends, however, impact local biota.

By interacting with many species in a variety of ways, introduced species affect, in an array of changes, the ecological communities. Interactions among the species are essential in the function of communities holding the interacting species together and determine their specific roles. The most prominent processes are competition, predation, parasitism, herbivory, and mutualism.

We need specific studies to characterise negative impacts qualitatively as well as quantitatively. With the present knowledge, all we can observe are the most immediate and obvious effects on local biodiversity and natural habitats. Introduced species in the Pantanal obviously rely on predation, browsing, competition for food, nest sites, in addition to potential transmission of diseases. One of these effects or the sum of them may alter community structure and function and habitat quality; in this case, for example, in terms of habitat loss by native species, due to environmental changes.

The negative impact of an exotic species on a population of native species of plants and animals is to reduce the population density of the vulnerable local species. In this case, the negative impact may cause a direct effect on the local species (competition for food or nesting site, for example) or adverse effects on habitat quality.

When an ecological community of interacting animals and plants are disrupted, invasive species can take advantage of the changed conditions to establish themselves. In some habitats of the Pantanal introduced species become part of the landscape, while others thrive at the expense of native species. In many cases the invasive species exerts additional stresses on the local and native species, with disruption to community structure and function. Since the invasive species does not have the natural predators from its original land to keep its numbers in check, it is able to spread throughout new habitats in the Pantanal. As soon as the invasive species of plant or animal becomes established, these invaders become hard to control. As we have seen in the cases of the feral pig *porco-monteiro* and the introduced Amazonian fish *tucunaré* they prey on or compete with native species. In terms of fauna, introduced African grass species drastically modify the species composition of open habitats of the Pantanal.

There is no specific control programme in the Pantanal to restore and prevent new invasions and keep established invasive species in check. Inside a broad conservation programme, there is the need to restore, protect and preserve natural habitats, including research into invasive species in ecological communities and ecosystems, to keep these established invaders under control.

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A conservation agenda for the Pantanal's biodiversity

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Abstract

The Pantanal's biodiversity constitutes a valuable natural resource, in economic, cultural, recreational, aesthetic, scientific and educational terms. The vegetation plus the seasonal productivity support a diverse and abundant fauna. Many endangered species occur in the region, and waterfowl are exceptionally abundant during the dry season. Losses of biodiversity and its associated natural habitats within the Pantanal occur as a result of unsustainable land use. Implementation of protected areas is only a part of the conservation strategy needed. We analyse biodiversity threats to the biome under seven major categories: 1) conversion of natural vegetation into pasture and agricultural crops, 2) destruction or degradation of habitat mainly due to wild fire, 3) overexploitation of species mainly by unsustainable fishing, 4) water pollution, 5) river flow modification with implantation of small hydroelectric plants, 6) unsustainable tourism, and 7) introduction of invasive exotic species.

Keywords: biodiversity, conservation, environmental threats, fauna, flora.

Uma agenda de conservação para a biodiversidade do Pantanal

Resumo

A biodiversidade do Pantanal constitui recurso natural com reconhecido valor na economia, na cultura, na recreação, na estética, na ciência e na educação. A vegetação, mais a produtividade sazonal, suporta uma fauna abundante. Muitas espécies ameaçadas de extinção ocorrem na região e aves aquáticas são excepcionalmente abundantes durante a estação seca. Perdas da biodiversidade do Pantanal e de seus hábitats naturais associados ocorrem como resultado do uso não sustentável da terra. A implementação de áreas protegidas é somente uma parte da estratégia necessária. Analisamos as ameaças ambientais do bioma sob sete tópicos principais: 1) conversão da vegetação natural em pasto e campos agrícolas; 2) destruição e degradação de hábitats, principalmente pelo emprego de fogo; 3) sobre uso de espécies, principalmente pela pesca; 4) poluição de água; 5) modificação de fluxo de rios, principalmente pela implantação de pequenas usinas hidrelétricas; 6) turismo não sustentável; e 7) introdução de espécies invasoras exóticas.

Palavras-chave: biodiversidade, conservação, ameaças ambientais, fauna, flora.

1. Introduction

As a wetland, the Pantanal is a biome characterised by constant or recurrent shallow flooding near the surface of the substrate, due to the low drainage capacity of its river system. This is the most remarkable feature of the Pantanal, with a dynamic that alternates annual cycles of droughts and floods, and determines the ecological interactions and patterns of biological diversity (Junk et al., 1989, 2006). The climatic and hydrological processes between plateau and surrounding plains are essential to maintain this water system, a fact that qualifies the Pantanal biome as a complex and unique system. The flood plain comprises approximately 60% of the geographical extent of the Upper Paraguay River Basin (Harris et al., 2005, 2006). Three major factors characterise the Pantanal wetland: water, substrate and biota (Alho, 2005). Most of the Pantanal fauna is widely distributed and endemic species are rare in the biome (Brown-Junior, 1984; Junk et al., 2006, Lourival et al., 2000).

The Pantanal is also characterised by a high density of various species of large vertebrates, with densities of populations that are not observed in any other biome in Brazil. Inventories carried out by Conservation International-Brazil showed average densities of 4.3 for alligators, 1.8 for capybaras, and 0.3 for marsh deer per square kilometre, population concentrations that provide an enormous potential for ecotourism and wildlife management (Willink et al., 2000). Similarly as for birds and mammals, the region has many species of fish with high populations, especially those whose food supply is based on organic material (Britski et al., 2007; Fernandes et al., 2009). Additionally, demographically healthy populations of many endangered species such as the Brazilian giant otter (*Pteronura brasiliensis*), the jaguar (*Panthera onca*) and the greater hyacinth macaw (*Anodorhynchus hyacinthinus*) are still viable in the Pantanal. These characteristics, combined with the high degree of conservation, are responsible for the inclusion of the Pantanal in the National Heritage List in the Brazilian Constitution of 1998 and the inclusion of the biome in the Ramsar Convention on Wetlands of International Importance (Willink et al., 2000; Alho, 2005); it is also considered one of the 37 major wilderness areas remaining on Earth (Mittermeier, 2002).

The region is formed by a complex mosaic of different kinds of habitats, strongly dependent on seasonal flooding. The present landscape arrangement and natural ecosystems are the result of three factors: 1) evolutionary changes occurring since the Quaternary, which probably influenced the drainage patterns of the region; 2) the pronounced differences in annual cycles of wet and dry seasons plus exceptional periods of long flooding or droughts causing retraction or expansion of the Pantanal, thus being a phenomenon related to greater or lesser primary productivity and ecological succession and 3) areas involving human intervention such as pastures, artificial ponds or introduced trees near the ranch houses (Alho, 2005).

As seen throughout this volume on articles describing the flora and fauna, the mixture of major vegetation formations that occur in the Pantanal has resulted in diverse and abundant fauna. The species which are able to exploit a wide range of resources have become both widespread and locally abundant.

The implementation of the Convention on Biological Diversity has continued since its conclusion in 1992 on the occasion of the UN Conference on Environment and Development in Rio de Janeiro. Although there are a number of conservation initiatives, including plans, programmes and projects such as "Priority Areas and Actions for Biodiversity Conservation - Cerrado and Pantanal = Áreas e Ações Prioritárias para Conservação da Biodiversidade - Cerrado e Pantanal" (MMA, 2007), a conservation synthesis on biodiversity status has been recently published worldwide (Millennium Ecosystem Assessment, 2005a-k). The third edition of *Global Biodiversity Outlook* (GBO-3), produced by the Convention on Biological Diversity (CBD) points out that the world has failed to meet its target of achieving a significant reduction in the rate of biodiversity loss by 2010 (Secretariat of the Convention on Biological Diversity, 2010).

The aim of this paper is to provide a concise review of the Pantanal's biodiversity conservation, discussing the environmental threats and suggesting conservation needs.

2. Methods

This article is based on two approaches: 1) literature review and 2) the experience of the authors with the biome, including scientific research combined with labour-management policies for scientific use and conservation of biodiversity in NGOs and government agencies, carried out in different regions within the considerable scale of time.

To list the endangered species in the Pantanal and surroundings, we consulted the IUCN Redlist (IUCN, 2010, CR = Critical Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened), and the official Brazilian List of Threatened Fauna (MMA, 2003) and threatened fishes and invertebrates (MMA, 2004).

3. Results and Discussion

The major challenge for the Pantanal is to meet the growing demand for social and economic development, mainly cattle ranching, agriculture, urban growth and tourism, while conserving biodiversity and providing essential ecosystem services for water quality, landscape integrity and wildlife protection.

These challenges are aligned with the development of new economic paradigms and environmental issues, which require – in addition to scientific knowledge and new technologies – innovative business models that valorise the natural capital and induce cultural changes. Natural Capital – providing ecosystems and biodiversity benefits for humankind – clearly underlies everything. Yet the annual loss of land-based Natural Capital – in terms of lost human welfare benefits from forest loss alone – has reached US$ 2 trillion to US$ 4.5 trillion (TEEB, 2010). Obviously, these innovative concepts are appropriate to the Pantanal and models of environmental evaluation should be customised for the region.

3.1. Threats

The major conservation problems of the Pantanal floodplain originate on the plateaus. The surrounding region has an important ecological role for the Pantanal, as it serves as source areas for the animal species and is essential in the maintenance of hydrological processes and the system of drought and floods (Brown-Junior, 1984; Willink et al., 2000). Consequently, preservation of the Pantanal is directly linked to preservation of the adjacent Cerrado. New trends in economic development are shown as the main threats to biodiversity in the Pantanal and its surroundings (Alho, 2008a; Harris et al., 2005, 2006; Junk and Cunha, 2005; Willink et al., 2000). Many farms have been established in the highlands surrounding the Pantanal and much of the natural vegetation (savanna) has been converted to soybean plantations or by other activities (Alho, 2005; CI et al., 2009). Among these problems are erosion, compacted soil, expansion of exotic pasture areas, silting rivers, pollution of water sources including by environmental contaminants (e.g. mercury), alterations in the water level, damming of rivers, and deposits of sewage and solid waste (Harris et al., 2005, 2006).

Deforestation, expanding agriculture, illegal fishing and hunting, unplanned tourism, and pollution by pesticides have also caused a progressive deterioration of natural habitats. Because of the huge demand for soybean plantations on the upland plateaus surrounding the Pantanal, the application of toxic agricultural chemicals is very common (Alho, 2005; Harris et al., 2005, 2006).

These environmental threats result in many endangered species, belonging to major taxa of Mammalia, Birds, Reptilia, Actinopterygii, Bivalves and Lepidoptera (Table 1). In the Pantanal, 20 species were from the official Brazilian List of Threatened Fauna (MMA, 2004) and threatened fishes and invertebrates (MMA 2004), and the IUCN listed four species in category "Endangered", eight "Vulnerable" and 17 "Near Threatened", while in the surrounding areas there were 22 species from the Brazilian List, and the IUCN showed one species "Critically Endangered", two "Endangered", seven "Vulnerable", and 18 "Near Threatened" (Table 1).

The environmental threats to the Pantanal's biodiversity can be grouped under seven interacting categories: 1) conversion of natural vegetation into pasture and agricultural crops, 2) destruction or degradation of habitat mainly due to wild fire, 3) overexploitation of species mainly by unsustainable fishing, 4) water pollution, 5) river flow modification with implantation of small hydroelectric plants, 6) unsustainable tourism, and 7) introduction of invasive exotic species. More recently, two other factors have proven devastating to populations and ecosystems, adding to the list: pathogen pollution, and global environmental change linked to climate (a direct effect on biodiversity and human health related to climate change is the likely increase in infectious diseases transmitted by insects or through contaminated water).

3.1.1. Conversion of natural vegetation into pasture and agricultural crops

A study carried out to present the results of monitoring changes in vegetation and land use in the Brazilian part of the Upper Paraguay River Basin (Bacia do Alto Paraguai) - BAP, (with a total area of 368,640 km²), considering the period from 2002 to 2008, showed that the region has been suffering the consequences of the expansion in cattle ranching and agricultural activities, especially in the highland region (CI et al., 2009). This study points out that while the Pantanal maintains 86.6% of its natural vegetation, the surrounding upland plateaus (*planaltos*) have kept only 41.8% of their original vegetation cover. During the short period from 2002 to 2008, the Brazilian side of the BAP lost 4% of its vegetation on the plateaus and 2.4% in the floodplain (the Pantanal). Data for 2008 show that cattle ranching is responsible for 11.1% of vegetation conversion in the Pantanal and 43.5% in the upland plateaus.

3.1.2. Destruction or degradation of habitat mainly due to wild fire

Fire is a major threat. Ranchers in the Pantanal set fire to the vegetation during the dry season as a "management" technique to "clear" the vegetation not used by cattle. The fire is initially started in the grassland but due to open areas, dry vegetation and wind, the fires often spread to savannas, woodland and forest (Alho, 2005). Removal of natural vegetation eliminates food and shelter, especially for forest-dwelling wildlife and epiphytic plants. Deforestation also increases erosion since most elevated areas have sandy soil that is easily blown or washed away by rain.

3.1.3. Overexploitation of species mainly by unsustainable fishing

Deforestation also affects fish since migration may be influenced by terrestrial habitat disturbances, mainly gallery forests and seasonally flooded fields. In the "*piracema*" – a kind of migration – the schools of fish move upstream at the beginning of the rainy season. Other migratory fish species leave the riverbed and move into the adjacent flooding areas searching for food.

Species of large fish such as jaw characins (*Salminus brasiliensis*), spotted surubim (*Pseudoplatystoma corruscans*), barred surubim (*Pseudoplatystoma fasciatum*), streaked prochilod (*Prochilodus lineatus*), "piraputanga" (*Brycon hilarii*) and threespot leporinus (*Leporinus friderici*) are some of the most remarkable Pantanal ichthyofauna (Menezes, 1994). This is due, in part, to the size of these

Table 1. Number of threatened species for the Pantanal and surroundings, based on IUCN Redlist (CR – Critical Endangered, EN – Endangered , VU – Vulnerable, NT – Near Threatened), and official Brazilian List of Threatened Fauna and Threatened Fish and Invertebrates (MMA, 2003, 2004).

Taxon	Pantanal					Surroundings				
	CR	EN	VU	NT	MMA	CR	EN	VU	NT	MMA
Mammals	0	1	5	10	13	0	1	5	9	13
Birds	0	3	3	7	7	1	1	1	9	4
Reptiles	0	0	0	0	0	0	0	1	0	0
Fishes	0	0	0	0	0	0	0	0	0	2
Bivalves	0	0	0	0	0	0	0	0	0	2
Lepidoptera	0	0	0	0	0	0	0	0	0	1
Total	0	4	8	17	20	1	2	7	18	22

large fish species that are valuable for professional and amateur fishing (Catella, 2004). Less evident and less known, but no less important, are the small fish species, which are up to 15 cm in length. Without the small characins, small catfish and small armored catfish, many large species could not exist: small species support aquatic food-chains, or are food-chain links, and essentially are fish whose biological richness is yet to be adequately evaluated, especially in the headwaters of the Pantanal (Sabino and Prado, 2006).

There is evidence of overfishing in some large fish species (Garcia, 2006), a major threat hanging over the water system of the Pantanal, which may adversely affect the flood pulse of the plain. About 70% of the water of the Pantanal wetland originates in the northern part of the basin, and the Cuiaba River, forming the main tributary of the Pantanal, contributes 40% of the water system (Brasil, 1997). Consequently, the information that 75% of all 115 dam projects planned for the Upper Paraguay basin (BAP) are in the northern region, in Mato Grosso State (ANEEL, 2010), gives a glimpse of a disturbing scenario since all these developments may change the hydrodynamics and floods in the wetland plain (Girard, 2002). A simple change in the regime of droughts and floods in this biome has already produced worrying results, since the main trigger for the reproduction of fish is the rise in river level with the first rains. Consequently, changes in this pattern negatively affect the reproductive cycle. When the fish run into an insuperable obstacle and a lake, their reproductive cycle is not completed because spawning occurs in the upper river (Godinho et al., 2009).

When dams are installed, conservation of the fish fauna, particularly migratory species, requires that connectivity is restored between the river channel and its flood areas (wetlands). Additionally, they are eco-hydrological studies which would be required in each river to assess the flow rates, in the flood period, timing of the spawning migration period and to ensure the survival of juvenile forms of fish (Calheiros et al., 2009).

3.1.4. Water pollution

The introduction of toxins and other contaminants to the Pantanal is an undesirable trend in habitat quality, since it affects valuable wildlife and fish resources as well as the quality of associated natural resources, including surface and ground water. The introduction of pollutants to ecosystems results in changes in an interrelated series of variables or processes that can affect the structure and function of the ecosystem in the short or long term.

Alho and Vieira (1997) point out that unregulated gold mining has contaminated Pantanal habitats with mercury. Fish samples showed high percentages of contamination (Cuiaba and Bento Gomes rivers) with mercury beyond the levels allowed by international standards for contamination. Bird species, which feed on fish, like the olivaceous cormorant *Phalacrocorax olivaceu*, the limpkin *Aramus guarauna* and the snail-kite *Rosthramus sociabilis* were also contaminated.

3.1.5. River flow modification with implantation of small hydroelectric plants on the upland plateaus

The floodplain is mainly formed by the tributaries from the left margin of the Paraguay River, in Brazil, with its western border following that of Brazil itself, touching Bolivia to the north and Paraguay to the south. The streams and rivers on these highlands are most prevalent where rainfall is ample, during the wet season. On the plateaus small brooks flow into small rivers, which flow into larger ones. The large rivers are shaped mainly by terrain, velocity of the water, levels of dissolved oxygen, nutrient loads, temperature and type of riverbed. The major rivers feeding the Pantanal are (from north to south): Paraguay, Bento Gomes, Cuiaba, São Lourenço-Itiquira, Taquari, Negro, Aquidauana-Miranda, Nabileque and Apa. These rivers are slow-moving when they meet the flatland and have coves with adjacent flood-land. They periodically overflow their banks. The maze of fluctuating water levels, nutrients, and wildlife forms a dynamic ecosystem. Flood-lands cover about 80% of the whole Pantanal. In contrast, during the dry season, most of the flooded areas stay dry, when the water returns to the river-beds (Alho, 2005, 2008a).

In particular, these changes may threaten water conservation in the main protected area and Ramsar Site, the Pantanal National Park. It is noteworthy that three quarters of these enterprises involve small hydro power-plants (PCH, from Portuguese acronym), located or planned for the same river, together resulting in an important impact. Even small power-plants, which may not form a reservoir, can change the discharge of nutrients and suspended matter and hence the cycling of nutrients in affected water bodies (Calheiros et al., 2009; Fernandes, 2010). Furthermore, the presence of the physical barrier in the form of a dam is known to prevent the movement of migratory fish species during the spawning season, affecting fish production in the medium and long term (Fernandes et al., 2009; Suzuki et al., 2009). All these changes and negative impacts on the water ecology of each sub-basin forming the Pantanal should be assessed simultaneously, in terms of the integrated area of the Upper Paraguay River Basin, prior to installing such projects (Calheiros et al., 2009).

3.1.6. Unsustainable tourism

Tourism, if well planned and regulated, provides an excellent alternative economy for the region. There is a booming tourist trade in the Pantanal. Unfortunately, most of this tourism is predatory. Tour groups may invade areas that should be preserved (e.g., waterfowl nesting grounds or rookeries), sport fishing groups may over-fish, in general spreading litter, particularly in illegal camp sites in gallery forest, where these fishermen leave signs of their predatory presence. Numerous tourist hotel boats throughout the Pantanal do not treat waste properly and spread solid waste on their way (Alho, 2005).

3.1.7. Introduction of invasive exotic species

Exotic species introduction has been one of the most important factors of biodiversity loss in the region, as discussed in a specific chapter of this volume.

3.2. Conservation agenda

Important comprehensive global analyses on biodiversity conservation and sustainable use have been produced and published: on the ecosystem and human well-being (Millennium Ecosystem Assessment, 2005a-k); on the importance of biodiversity in human health (Chivian and Bernstein, 2008); on the implementation of the objectives of the Convention on Biological Diversity (Secretariat of the Convention on Biological Diversity, 2010).

Biodiversity plays a fundamental role as ecosystem services in the maintenance of natural ecological processes. The economic or utilitarian values of biodiversity rely upon the dependence of man on biodiversity, involving the products that nature can provide: fishing resources, tourism and extractive products. It also encompasses ecosystem services, such as climate regulation, reproductive and feeding habitats for commercial fish, some organisms that can create soil fertility through complex cycles and interactions, such as earthworms, termites and bacteria, in addition to the fungi responsible for cycling nutrients like nitrogen, phosphorus and sulfur and making them available for plant absorption. These services are the benefits that people indirectly receive from natural ecosystem functions (air quality maintenance, regional climate, water quality, nutrient cycling, reproductive habitats of commercial fish, etc.) with their related economic values (Alho, 2008b).

The following conceptual levels of ecosystem are important in the Pantanal:

- Species diversity - the number of species found in a given study area or in a kind of habitat. Although the species diversity of the Pantanal is not high in comparison to other Brazilian biomes, the abundance of species, including endangered species, is high.
- Functional diversity - the web of functions that are performed by species in a system, for example, the role of gallery forest for arboreal mammals, and the rhythms of seasonal production of food (shoots, flowers and fruits) for arboreal primates. Also includes feeding guilds of waterfowl observed in the Pantanal.
- Genetic diversity - genetic variability within a species, that is, variation among individuals or populations.
- Community and ecosystem diversity - assemblages of interacting different species also interacting with abiotic components of the environment, such as the *cordilheira* habitat of the Pantanal.
- Habitat diversity - characteristics of a given area where species, population and communities occur. The Pantanal has a great variety of different kinds of habitats. Alteration and loss of natural habitat is one of the most severe negative impacts on biodiversity.

Traditionally, the conservation agenda employs the implementation of conservation units in selected priority areas, with relevant biological attributes. This has been shown to be insufficient. The agenda needs to include other approaches, such as economic incentives that would induce stakeholders to adopt initiatives that balance economic interest and nature protection. In the Pantanal there is enormous potential for ecotourism or well-planned tourism in the wild.

Wildlife watching, particularly ecotourism, is a form of tourism based on the principles of making an active contribution to the conservation of the natural and cultural legacy and interpreting the region's natural and cultural heritage for visitors. Ecotourism is often based on relatively low levels of tourism in an area, and is therefore particularly suited to organised tours for small groups, and also for independent travelers. In the Pantanal planning for this kind of operation must increase to help local communities generate sustainable income and employment. To be sustainable, tourism needs to make a positive contribution to the natural and cultural environment, generate benefits for the host communities, not put at risk the future livelihood of local people, and to make every effort to anticipate and prevent economic, environmental, social and cultural degradation (Tapper, 2006).

Wildlife watching tourism in the Pantanal needs to integrate considerations of sustainable development into the way in which it is operated and managed, and combine efforts for environmental education, including the construction of facilities for visitors, such as a public aquarium, thus improving the structure of environmental interpretation. Wildlife watching tourism also involves appropriately operated tourism activities that include local communities, wildlife managers in public and private sectors, national and local government, conservation NGOs (particularly wildlife societies which have a role in popularizing and raising awareness about wildlife and conservation). The tourism sector includes tour operators, local operators, excursion providers, accommodation and, of course, the tourists themselves (Cochrane, 2003; Tapper, 2006).

A wide range of recommendations should also be offered to managers of the environmental and water resources of the two states in which the Pantanal is located (Mato Grosso and Mato Grosso do Sul), and managers of Brazilian electric sector. The decision makers need to be made aware of the fragility of the biome and the effect of changes in hydrological cycles arising from construction of small dams for hydroelectricity. Among the suggestions, particularly urgent is an Integrated Environmental Assessment on the impacts of the use of electric power from the Alto Paraguay (Calheiros et al., 2009). Reports focused on basins north of the BAP show that the migration of fish was negatively affected at several points, compromising their reproduction and distribution in the Pantanal. When faced with unsatisfactory conditions for their survival, some fish species tend to decrease in number or size and even disappear, especially migratory species (Calheiros et al., 2009). Based on the available scientific information on the basin of the Upper Paraguay and Pantanal, specific guidelines for the sustainability of the region must be formulated (e.g., Conservation Plan of the Upper Paraguay Basin - PCBAP, Fund for Global Environment and Global Environment Facility - GEF Alto Paraguay, among others) for the conservation of ecological processes that govern the functioning of this biome. One way to ensure the ecological processes of fish fauna is to keep some sub-basins of the BAP free from any dams (Calheiros et al., 2009).

However, conservation involves combining both natural ecosystems and human societies, and conservationists deal with systems that are extremely complex and fragile, as is the case of the Pantanal. Sometimes, the urgent nature of the problem demands that the stakeholder take immediate action in their own interests, despite the risks inherent in the lack of certainty about how best to proceed.

Protected areas are a basis of conservation policies and provide multiple benefits. There are over 120,000 designated protected areas covering around 13.9% of the Earth's land surface. Despite its importance, just 0.55% of an area of 140,000 km^2 - only in Brazil – of the Pantanal is protected by federal conservation units (Harris et al., 2006).

On a global scale, there has been a positive assessment of the implementation of public policies on science and technology for the use and conservation of biodiversity (Millennium Ecosystem Assessment, 2003, 2005a-k). The success of these actions was made possible by unprecedented international cooperation among taxonomists from a wide range of research institutions and collections, including museums and herbaria, universities, botanical gardens and collections of biological resources (Higushi, 2006). This is still a drop in the ocean, considering the challenges facing the Pantanal and surroundings. Fortunately, recent investments, which include the creation of research programmes (e.g., Rede Centro-Oeste and SisBiota, from the Ministry of Science and Technology, and Biota-MS Programme, from Mato Grosso do Sul State) and institutions (e.g., National Institute of Wetlands, the INAU) look set to reverse this situation in Brazil. In the medium and long term, to expand and strengthen these coordinated scientific networks, it is necessary to build and maintain long-term biodiversity research programmes in the Pantanal, based on liaison between regional and national entities that work with biodiversity.

Priority topics and guidelines for conservation:

Environmental issues

Land use, soil conservation and management

1) Promote agricultural practices for soil use that avoid loss of soil, including erosion.
2) Promote economic activities related to the objectives of the protected areas' buffer zones and experimental projects for extractive reserves.

Water resources

1) Develop mandatory requirements for integrated studies on environmental impact of large development projects, such as waterways.
2) Secure the control of environmental contaminants, including pesticides, according to international protocols.
3) Enforce the existing legislation on water resources, including their springs.
4) Consider the hydrological basin and micro basin as a conservation unit or ecosystem.
5) Implement the effective participation of the Basin Committees in order to enforce legislation.
6) Promote the conservation of wetlands that within the framework of the Ramsar Convention.

Air pollution and climatic change

1) Establish shared management between Government agencies and civil society to control wildfire.
2) Conduct technical training, environmental education, and campaigns to prevent and combat wildfire.
3) Carry out environmental restoration in degraded areas for carbon absorption (carbon capture), among other benefits.

Biodiversity: conservation, research and sustainable use

1) Promote the expansion of protected areas, ideally to reach 10% of the region as intended by the Government (40% of indirect use conservation units and 60% of direct use).
2) Secure land ownership in protected areas, the development of their management plan and its effective implementation, including the necessary staff.
3) Target priority incentives for the creation of private reserves (RPPN).
4) Promote incentives for the implementation of ecological sales taxes (ICMS Ecológico).
5) Undertake the administration of bioregional areas including the concept of ecoregions and biosphere reserves.
6) Carry out experimental pilot projects for sustainable use in protected areas of direct use.
7) Provide incentives for the creation of ex-situ reserves.
8) Provide incentives for sustainable use of biological resources including wildlife.
9) Promote the certification of products from sustainable use programmes.

Scientific and technological issues

Research and technology

1) Support shared participation between Government and the private sector, aiming at the achievement of innovative technologies.

2) Promote basic and applied research for the sustainable use of resources and technological practices for sustainable development.

Institutional issues

Institutional strength and shared management

1) Integrate information and actions of institutions engaged in conservation of the region.
2) Promote government policies to implement organisational strength including infrastructure, personnel, programmes and dissemination of results.

Legal and economic instruments

1) Integrate sectoral policies in order to promote regional conservation and development.
2) Create incentives for shared environmental management at all levels.
3) Promote law enforcement.
4) Implement ecological-economic zoning.

Social-cultural issues

Land use, territorial expansion with new agricultural frontiers

Produce guidelines for implementing ecological-economic zoning through shared participation and development indicators for sustainability.

Urban and metropolitan expansions

Develop means to control urban migration.

Poverty and life quality

Develop programmes to support health and education for better quality of life.

Cultural diversity and traditions

Recognise the value of ethno-cultural diversity and traditional knowledge for conservation and sustainable use of resources.

Communication and environmental education.

Plan, regulate and implement programmes on environmental education to spread and consolidate the education process of local people and to disseminate information through modern means of communication.

Economic issues

Mineral exploitation

1) Conduct sustainable mining.
2) Create environmental certification for mining.
3) Integrate the process of authorisation, law enforcement, and control of mining.

Eco-business and sustainable tourism

1) Develop incentives for sustainable use of biodiversity.
2) Develop incentives for sustainable tourism.
3) Create tourist facilities, such as public aquariums and zoos, to disseminate biodiversity information by means of environmental education programmes.

Infrastructure

1) Harmonise planning and implementation of infrastructure, mainly for transport and energy, with recommendations for ecological-economic zoning, as well as undertaking reliable studies on environmental impact for each case.

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Concluding remarks: overall impacts on biodiversity and future perspectives for conservation in the Pantanal biome

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Abstract

The Pantanal biome is characterised by seasonal flooding which determines specific ecosystem processes, with the occurrence of adapted plants and animals to the annual shrinking and expansion of habitats due to the seasonal hydrological regime. Biodiversity abundance varies during the dry and wet seasons. The Pantanal's biodiversity is a fundamental component of ecosystem services for human society, including nutrient cycling, fish production, ecotourism, carbon storage, flood control, among others, which are relevant to regional and global environmental consequences. The biome has been impacted by the conversion of natural vegetation into agricultural fields and pasture for cattle raising, with alteration and loss of natural habitats and biodiversity. Major negative impacts occur in uplands, with drastic deforestation of savanna vegetation, where main rivers feeding the Pantanal have their springs. This article discusses future needs and priorities for ecological research, in order to better understand the biome's natural system, to achieve conservation and sustainable use.

Keywords: biodiversity, conservation, environmental impacts, habitats, Pantanal.

Observações conclusivas: impactos ambientais sobre a biodiversidade e perspectivas futuras para conservação no bioma Pantanal

Resumo

O bioma Pantanal é caracterizado pela inundação sazonal que determina processos ecossistêmicos específicos, com a ocorrência de plantas e animais adaptados à mudança anual de encolhimento e expansão de hábitats em virtude do regime hidrológico sazonal. A biodiversidade do Pantanal é um componente fundamental dos serviços ecossistêmicos prestados à sociedade humana, que inclui reciclagem de nutrientes, produção pesqueira, ecoturismo, resgate de carbono, controle de enchentes, entre outros, que são importantes consequências ambientais em nível regional e global. O bioma tem sido afetado pelo impacto da conversão de sua vegetação natural em campos agrícolas e pasto para a pecuária, com alteração e perda de hábitats e biodiversidade. O impacto maior tem ocorrido nas terras altas do planalto do entorno da planície, com desmatamento do Cerrado nas áreas onde nascem os rios que alimentam o Pantanal. Este artigo discute as necessidades e prioridades futuras de pesquisa ecológica para melhor entender o ecossistema e, assim, atingir sua conservação e uso sustentável.

Palavras-chave: biodiversidade, conservação, impactos ambientais, hábitats, Pantanal.

1. Land Use

The loss of natural habitats and their associated biodiversity in the Pantanal have been drastic during the last decades, particularly in the upland region of the *Cerrado* plateaus surrounding the flooding plain (Silva et al., 2010; Conservação Internacional, 2009). The study by Silva et al. (2010) analysed the deforestation of the Pantanal and its surroundings over the past 30 years. Deforestation in the Pantanal increased about 20 times in the period, reaching near 15-20% of its area. Deforestation in the Upper Paraguay River Basin reached more than 40%. The Pantanal still retains about 80% of its natural vegetation, but the upper reaches of the Paraguay River basin have lost about 60% of its natural vegetation cover, with a higher rate of deforestation in the highland areas of the basin.

Agriculture (mainly soybean) and cattle ranching is prevalent in highlands but in the northern region of the river basin, mining has been active since the beginning of the XVIII century (Casarin, 2007). Mining is responsible for environmental degradation in the region of the Paraguay/Diamantino watershed, resulting in erosion with revolved soil due to mining processing. In addition, deforestation for agriculture and cattle pasture cause erosion mainly in slope terrains and mountain hillsides of the highlands.

While at the international level, the Ramsar Convention on Wetlands was established to protect wetlands, on the national level, Brazil has signed the Convention and designated the Pantanal as a Ramsar site. On the other hand, Brazilian environmental legislation has been recognised as updated, but difficult to enforce due to a weak environmental institutional structure, mainly in the two states (Mato Grosso and Mato Grosso do Sul) which comprises the Pantanal.

1.1. Environmental impacts affecting biodiversity

The Pantanal has been negatively impacted by unsustainable socio-economic development through predatory land use (Alho, 2005). Major economic activities are cattle ranching, fishing, agriculture, mining and tourism. Deforestation to convert natural habitats with pastures for cattle is increasing. The consequence is loss of biodiversity, for example, removal of forest that eliminates food and shelter, for forest-dwelling wildlife. Environmental pollutants are introduced from uncontrolled use of pesticides and herbicides, contamination with mercury from unregulated gold mining, urban liquid and solid waste, including untreated sewage, introduction of invasive exotic species, unsustainable tourism, illegal hunting, traffic of wildlife, soil degradation, lack of education and environmental consciousness, and fragility of environmental organizations to enhance legislation.

1.2. Needs to identify, evaluate and mitigate environmental impacts

Future development projects that affect the biome's biodiversity should only be undertaken after proper and thorough environment assessment procedures, based on specific terms of reference and public participation. Establishment of scoping to identify which potential impacts are relevant to assess, based on legislation, international conventions, technical and scientific knowledge and public involvement, to correct analysis to license projects or to reject them.

Brazilian public attitudes toward nature in general, and biodiversity in particular, have improved, and there has been more drive to protect the Pantanal. It would constitute progress to protect the ecological relationship between the floodplain, which is the Pantanal, and its surrounding upland plateaus, to apply environmental flow assessment (EFA) in any development project that affects river flow. This should apply for the hydroelectric plants being established in rivers that feed the Pantanal. This procedure should determine how much of the natural flow regime of a given river should continue to flow down to the Pantanal floodplain in order to maintain ecosystem processes. If on the one hand, development projects are good for the region, on the other, conservation priorities have to be carried out in order to fulfill ecological needs.

2. Research Priorities

It has become evident, because of the importance of the Pantanal biome, that scientific research is needed to improve conservation on the basis of scientific methods, in order to discuss the progress, problems and priorities to achieve sustainable use in the region. Scientific research improves our understanding of the magnitude of biodiversity, land use, and contributes to mitigating land use impacts. Incorporating research results into an action plan for biodiversity conservation of the Pantanal is an important part of the adaptive management process. The following are identified research priority topics for science-based conservation, protection and management:

- Studies on ecological processes to better understand the function of natural ecosystems;
- Hydrology studies to establish the relationship and dependence of river flow from highlands to floodplain in connection to the kinds of habitats and their associated biodiversity;
- Studies on fish movement, dispersal of semi-aquatic and aquatic mammals and other organisms, in relation to flooding regime to determine their significance and sensitivity to hydrological seasonal events and offer of ecological resources;
- Emphasis on the magnitude of the biodiversity, including ecological parameters such as species richness and species diversity of all types of wild plants and animals;
- Studies on habitats and microhabitats requirements and selection for wildlife in relation to seasonal offer of resources;
- Conservation action including protected areas, ecological corridors; feeding and reproductive niches of wildlife;
- Effects of habitat heterogeneity and other landscape factors on demography and recruitment of indicator species of insects, herpetofauna, fish, birds and mammals;
- Need to understand the effect of ecological processes on biodiversity responses (ecological parameters and behavioural patterns) to factors measured in different kinds of habitats and at landscape scales;
- Dispersal movements of wildlife, including fish, amphibians, reptiles, birds and mammals between feeding niches and reproductive niches as a function of seasonal annual variation;
- Migration routes especially of bird species;
- Studies on feeding and reproductive guilds of birds and bats;
- Habitat selection and microhabitats of small mammals (rodents and marsupials);
- Studies on environmental components selected by small mammals in relation to habitat selection and microhabitat types;

- Identification and analyses of bioindicators for habitat quality and for degrees of disturbances;
- Studies on ecological communities structure and function in relation to ecological processes of the Pantanal;
- Considerations on consumptive and non-consumptive activities in the Pantanal as a means of improving ecotourism to achieve sustainable use of the biodiversity.
- Identification and evaluation of impacts and development of alternatives, to predict and identify environmental impacts of proposed projects;
- Monitoring, enforcement and environmental auditing mitigation projects to verify the compliance of proponents to ensure mitigation and compensation impacts according to Federal and State legislation;
- Impact of invasive exotic species on population, community and ecosystem structure and function;
- Identification and analysis of categories of activities known to cause biodiversity impacts including ecotourism;
- Studies on priority areas for conservation, including production of maps indicating conservation categories according to Brazilian legislation; areas where impact assessment at an appropriate level is required; areas containing threatened ecosystems outside of formally protected areas; areas identified as being important for the maintenance of key ecological processes; areas known to be habitat for threatened species; areas identified as important cultural and spiritual components.
- Establishment of the cause and effect relationship between land use activities and biodiversity, with focus on: indicator species, human-caused impacts and aquatic integrity (macro-invertebrates as indicators); fish habitats and fishery; aquatic and semi-aquatic mammal species and dispersal in function of flooding regime; water quality indicators, and other contaminant indicators in relation to aquatic health;
- Establishment of benchmark conditions for regional sustainable development indicators for ecotourism and recreational areas;
- Research on climate change related risks in relationship to biodiversity and ecosystem integrity.

2.1. Ecosystem services in connection with human well-being and research opportunities

Ecosystem processes of the Pantanal maintain biodiversity by providing habitats for many plant and animal species. These processes produce products such as fish and other extractive resources. As a wetland, the biome is a productive ecosystem, providing seasonal nutrients for biodiversity. In addition to unsustainable land use and increasing economic development resulting in degradation of natural habitats, the Pantanal is also facing other threats including the consequences of climate change.

Independent of human benefit or intervention, an ecosystem works as an interdependent system in nature and biodiversity is an important component of this holistic system. However, during recent years, several published reports emphasise the role of ecosystem services for human being as a tool to apply conservation and protection (Costanza et al., 1997; Daily, 1997; Daily et al., 1997; Balmford et al., 2002; De Groot et al., 2002; Millenium Ecosystem Assessment, 2005a-k; Alho, 2008; Chivian and Bernstein, 2008; Mindell, 2009; Keddy et al., 2009; Cardinale et al., 2009). The concept of ecosystem services implies function and ecosystem processes, meaning the conditions through which natural ecosystems and biodiversity, that integrates the system, sustain and fulfill human life.

Ecosystem services are the benefits provided to humans as a function of ecosystem processes, like water quality, pure air, geobiochemical cycling of nutrients for plants and animals including importance for agriculture, wood, food, medicine and so on. It is the capacity of ecosystem processes to provide services and goods that satisfy human needs. These ecosystem processes are interactions among elements of the ecosystem or ecological attributes (physical, like solar energy and soil; chemical, like photosynthesis and cycling of nutrients; biotic, like primary production and secondary production, food chain and behavioral interactions) that are valued by humans.

The following ecosystem services of the Pantanal illustrate the importance of protected nature and show the relevance for scientific research:

- **River flow**. Natural river flows of hydrological cycles are fundamental for drainage, river discharge and seasonal inundation that influence habitats and biodiversity. They provide water quality for human consumption and nutrients for fishery.
- **Nutrient cycling**. Carbon, oxygen, hydrogen, nitrogen, phosphorus are cycled in ecosystems. Decomposition by soil organisms releases these and other elements into the soil and atmosphere so they can be used again. Nutrient cycling provides productive soil. Ecological processes play a role in storing and recycling organic matter, nutrients and human waste.
- **Fishery**. Fish is an important economic element of the Pantanal. Feeding and reproductive habitats of commercial fish depend on natural ecosystems.
- **Aesthetic, recreation and cultural attributes.** There is an increasing touristic industry in the Pantanal. People are attracted to the region by its natural scenery and beautiful landscapes. Bird watching has become internationally popular in the region and natural ecosystems are often used as places for recreation, including sport fishing. The biome also offers cultural traditions and folklore.

- **Medicinal and genetic attributes**. The biome's biodiversity offers a diversity of life forms to be cultivated as crops and domesticated animals and also material for biotechnological experiments. It provides material for synthetic drugs used as medicines.
- **Natural habitats and biodiversity**. The Pantanal's natural systems provide living space for plants and animals which characterise its exuberant biodiversity, including genetic diversity. The different kinds of vegetation cover provide suitable shelters and other ecological resources to support a diversity of animal life. The heterogeneity of life forms is essential for maintaining all other ecosystem functions and services, as a result of millions of years of biological evolution. Maintenance of biodiversity is supported by natural ecosystems within such a large biome as is the case of the Pantanal. The biome's current order of its biodiversity magnitude depends upon its size (near 140,000 km²) and the heterogeneity of its different kinds of natural habitats. Vegetation cover prevents soil erosion and sediment control. It also works on fixation of solar energy and biomass production.
- **Scientific attributes**. The Pantanal offers numerous opportunities for scientific research, environmental education and monitoring environmental changes due to human occupation and impacts of development projects.
- **Climate change**. Vegetation cover, evaporation, regional and continental circulation patterns, like *El Niño* and *La Niña*, and water bodies, all interact to determine weather and climate. Seasonally flooded areas can be carbon sinks, which influence global climate change. The regional soil is composed of partially decayed accumulations of plants, and other organisms, resulting in stored carbon. The removal of carbon from the atmosphere depends on that carbon storage and vegetation cover. Estimates for the annual carbon accumulation in the Pantanal are not known, but the biome may play a significant role in the sequestration of carbon. There is a concerning trend about the future of Brazilian biomes regarding climate changing and the ecosystem processes. According to the United Nations Climate Change Conference held in Cancún, Mexico, in November-December 2010, studies on climate and hydrologic models in the Cerrado river basins pointed out toward a reduction of 20-25% of annual precipitation in 2100, leading to a decrease of 7-10% in the volume of recharge of aquifers and in the river discharges, depending on the analysed scenario.

Ecosystem services provided by the Pantanal include maintenance of biodiversity, landscape, freshwater supply, fishery, nutrient cycling. These ecosystem services contribute to human quality of life. This important Brazilian biome requires sustainable management for its use and economic development, built on a new approach for the future, considering the inseparable relationship between economic development and human well-being to achieve sustainability. Scientific research can pave the way to reach this objective. Due to the rapid rate of environmental degradation, including altered hydrology, with loss of natural habitats and biodiversity, management strategies are imperative and urgent.

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