SNAKES OF THE PANTANAL: BIOGEOGRAPHY AND TAXONOMIC, PHYLOGENETIC AND ECOMORPHOLOGICAL DIVERSITY

SERPENTES DO PANTANAL: DIVERSIDADE TAXONÔMICA, FILOGENÉTICA E ECOMORFOLÓGICA

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Snakes of the Pantanal: biogeography and taxonomic, phylogenetic and ecomorphological diversity

Serpentes do Pantanal: diversidade taxonômica, filogenética e ecomorfológica

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RESUMO

A composição de comunidades biológicas atuais é resultado da interação da história evolutiva dos organismos e dos ambientes com fatores locais contemporâneos que mediam a ocorrência e coexistência das espécies. Em planícies de inundação como o Pantanal, os pulsos de inundação são considerados as principais forças que mediam processos ecológicos, que por sua vez controlam a distribuição espacial e temporal dos organismos e a composição das comunidades. O Pantanal é a maior planície de inundação tropical e possui uma biota menos rica que a encontrada em áreas de entorno. Isto tem sido atribuído as condições adversas que os ciclos de inundações impõem sobre os organismos, e também à recente formação da região. O principal objetivo desta tese foi investigar os padrões de diversidade de comunidades de serpentes no Pantanal a respeito de suas origens, apresentando e testando hipóteses sobre processos passados e atuais que operaram na organização de comunidades de serpentes dessa planície inundável. Nós adotamos abordagens que podem evidenciar processos em escalas temporais recentes e antigas, e uma escala espacial ampla, que abrange toda a bacia hidrográfica onde o Pantanal está situado – a bacia do Rio Paraguai. Nós encontramos que a fauna de serpentes do Pantanal é parte de uma conjunto de espécies amplamente distribuído na bacia, que é relacionado à calha do Rio Paraguai e às planícies associadas a ele. A bacia hidrográfica possui faunas regionalizadas distribuídas ao redor da planície do Pantanal, a qual pode estar atuando como barreira para algumas espécies e como corredor de dispersão para outras. Nossa expectativa de que as inundações sazonais ajam como filtro ambiental, permitindo a ocorrência na planícicie somente das espécies com adaptações para lidar com esses eventos periódicos, não foi suportada. Ao invés disso, as inundações parecem diminuir a força relativa dos processos determinísticos na organização das comunidades e então favorecem a ocorrência de espécies com hábitos generalistas por causarem distúrbios recorrentes no ecossistema. Filtros ambientais podem estar em ação por meio do gradiente de cobertura

de florestas, dando origem a comunidades mais ricas em áreas mais abertas e taxocenoses formadas por espécies com uso de hábitat similares em áreas mais florestadas. Porém esses padrões podem igualmente terem sido produzidos a partir das divergências ecológicas observadas entre as biotas que se originaram em áreas abertas e florestadas da América do Sul, e não pela ação isolada de um filtro ambiental.

ABSTRACT

Species composition in biological communities is a result of interactions of the evolutionary history of both organisms and environments, along with local factors that currently mediate species occurrence and coexistence. In floodplains, like the Pantanal, flood pulses are recognized as the main driver of ecological processes that control both species spatial and temporal distribution, but also shape communities. The Pantanal is the largest tropical floodplain on Earth and it has a less rich biota than that of surrounding regions. This has been attributed to the hardness imposed by the flood cycles on the organisms and also to the recent formation of the plain. The main goal of this thesis was to investigate diversity patterns of the snake community of the Pantanal regarding their origins, through stating and testing hypothesis about past and present processes that acted on the current assembly of snake communities in this seasonal floodplain. We adopted approaches that provided evidences for processes at deep and recent time scales, as well as a wide special scale, that encompasses the entire hydrographic basin where the Pantanal is located – the Paraguay River Basin. We found that Pantanal snake fauna belongs to a species group widely distributed in the basin, and is linked to the Paraguay River channel and nearby lowland areas. The entire basin has regionalized faunas distributed around the Pantanal floodplain, which may be acting as a barrier for some species and as a dispersal corridor for others. Our expectation that seasonal flooding could act as an environmental filter, allowing only species with adaptations to deal with this recurrent event to occur, was not supported. Rather than

that, flooding seemed to be decreasing the relative force of deterministic processes on community assembly and so favoring species with generalist habits by promoting recurrent ecosystem disturbances. Environmental filter can be acting through the forest cover gradient, giving origin to richer communities in more open areas and assemblages formed by species with similar habitat uses in more forested aeras. However, these patterns also could have originated from the ecological divergences between biotas originating from open and forested areas in South America.

GENERAL INTRODUCTION

The Pantanal, the largest wetland on Earth, is located in central South America [1, 2]. The physical and biological aspects of this floodplain seem strongly related to its annual cycles of floods and droughts: flooding provides a permanent exchange of water, sediments, chemical components, and organisms between the main river channels and adjacent areas [1]; the vegetation is distributed over a flooding gradient, in accordance to tolerance to either flood or drought [3]; and animal communities experience shrinking and expansion of habitats related to the flooding pulse and adapt their natural history or behavior to it [4]. Because the Pantanal is a converging point of several South American ecoregions [2], representatives from other biotas are found in the floodplain along with species that have wide distributions, and often they establish large populations in the floodplain [5]. Notwithstanding, in general the Pantanal biota is less rich than that of surrounding regions, and thus far no endemisms have been confirmed in the floodplain. This lack of endemicity and decreased richness have been attributed to the harshness imposed by the seasonal cycles on the organisms and also to the recent formation of the Pantanal [2, 3, 4, 5].

The main phase of subsidence that resulted in the wetland depression occurred during the transition between the Pliocene and Pleistocene, about 2.5 million years ago [6]. The vast plain that resulted from this event nowadays stores water originating from the

77 surrounding upland regions, and delivers it slowly to the lower sections of the basin. Due to
78 the very low declivity of the terrain, during the rainy season water overflows the main river
79 channels and flows slowly from east to west in permanent and temporary streams and then
80 southward upon entering the Paraguay River [1, 7, 8]. Seasonal fluctuations in water level
81 generally range from 2 to 5 m in the Paraguay River, but typically have lower values across
82 the Pantanal plains, with flooding taking from 3 to 6 months to move across the whole
83 floodplain [1, 7, 8].

84 In floodplains like the Pantanal, the flood pulses drive important seasonal ecosystem
85 changes [9, 10], activating ecological processes that control both the spatial and temporal
86 distribution of organisms as well as their life-history strategies. River flow regime
87 adaptations range from behaviors that result in the avoidance of individual floods or
88 droughts, to morphological changes and life cycles that are synchronized with long-term
89 flood patterns [11, 12, 13]. The adverse effects from flooding are responsible for changes in
90 distribution and species composition for several taxa in many regions [4, 11, 14, 15, 16, 17].
91 Researchers have argued that stressful environments, such as seasonally flooded areas, can
92 act as environmental filters [11, 14, 18]. When this occurs, biological communities of these
93 areas are composed only of organisms exhibiting adaptations to deal with the stressful
94 conditions found there, and species in the regional pool that are not adapted to area's
95 conditions are excluded.

96 Environmental filters are one of the processes that assemble biological
97 communities. In addition to them, species interactions, such as competition, also play a role
98 in structuring of local assemblages [19]. The resultant patterns of filter process are
99 communities composed by more similar species than expected considering the regionally
100 available species pool, because these organisms have the same traits needed for
101 maintaining viable populations in the habitat where the community was established [20]. On
102 the other hand, when interispecific competition is the main force in the assembling of

103 communities, these will be composed by species with divergent traits, which allows them to
104 use available resources in different ways and co-occur in areas with limited resources [20].
105 Additionally to these deterministic forces, community assembly can be simultaneously
106 influenced by factors that are relatively more stochastic, which include unpredictable
107 disturbance, probabilistic dispersal and random birth-death events [21, 22]. These events act
108 equally on organisms despite their taxonomic identity and result in local communities that
109 are a random subsets of the regional species pool present on larger spatial scales [23].

110 In turn, the diversity patterns observed in regional species pools often are more
111 influenced by historic process that occur at larges scales of time and space, such as species
112 immigration, speciation, and extinction [24]. By the action of theses forces it is possible that
113 regional communities may only contain a subset of the diversity from the areas of origin, or
114 may have diversified with particular ecological tendencies, which constrain the range of
115 possible outcomes that local processes could produce [25]. So, species distributions are
116 shaped by the interplay between evolutionary and ecological processes and one of the
117 major challenges in ecology remains in identifying the processes that regulate species
118 composition in different communities and their relative forces [21, 22, 24].

119 The knowledge about current snakes communities in the Neotropics highlights the
120 strong influence of historical process, such as origin and dispersion of particular clades, on
121 the composition of local assemblages [26, 27, 28]. The three main South American snake
122 lineages have distinct geographic distribution patterns, in consequence, communities from
123 different locations have divergent patterns of species dominance and resource use [26]. But
124 the action of current ecological processes, such as environmental filters, on the diversity of
125 Brazilian snake communities also was evidenced recently: communities from open areas
126 tend to be more clustered than those from forested areas because open areas constrains
127 the occurrence of species with arboreal habitats [29]. Information on snakes of the Pantanal
128 floodplain are yet scarce. Similarly to other organisms, the snake fauna is mixture of the

129 elements from the surrounding ecoregions, with lower species richness and no endemism
130 [30, 31, 32]. Local community composition follows the expected dominance of Dipsadidae
131 species due to the history of Neotropical snake clades, and is more similar to open domains,
132 such as the Cerrado and the Chaco, than to neighboring forested areas [30, 31, 32]. Despite
133 the hypothesis of environmental similarity with open ecoregions and restrictions imposed by
134 flooding have benn often indicated as primary causers of the recorded diversity patterns,
135 the processes involved in the assembly of Pantanal snake communities, locallly and
136 regionally, have not yet been formally addressed.

137 By characterizing phylogenetic relationships among species within a particular
138 community and among communities, in relation to the regional pool and along with analyses
139 of functional diversity of the assemblages, it is possible to detect the ecological processes
140 that were important in creating the current structure observed in local communities, which
141 species traits these forces act on, and through which, if any, environmental feature they are
142 operating [19, 20, 21, 22]. And through the study of the regional distribution of species
143 associated with particular areas and biogeographical events, it is possible to investigate
144 processes on larger spatial and temporal scales, generating hypotheses about the origin and
145 dispersion of the biota in a particular region [33, 34].

146 In this context, the main goal of this dissertation was to investigate the patterns of
147 diversity of snakes in the Pantanal wetland regarding their origins, presenting and testing
148 hypothesis about past and present processes that acted on the assemblage of current
149 communities of this seasonal floodplain. Considering that the structure of biological
150 communities can be seen as an aggregate property of phenomena on different scales of
151 time and space [24, 35] we adopted approaches that can evidence processes acting on deep
152 and recent time scales, and a wide spacial scale, that encompasses the entire Paraguay River
153 Basin the hydrographic basin where the Pantanal is located. This work is divided in three
154 chapters in the format of scientific papers following the style and organization indicated by

155 the journal PLOS One. We dedicated the first chapter to a more historical examination,
156 trying to discover whether the snake fauna that occurs in and around the Pantanal
157 floodplain has divergent biogeographical origins and whether the rise of the Pantanal
158 affected the ancestral biota of the region. In the second chapter we searched for
159 environmental and historical factors that drove the turnover of species between different
160 communities inside and outside the Pantanal, in the Paraguay River Basin. And in the third
161 chapter we analyzed the functional and phenotypical structure of these communities to
162 investigate if flooding or other environmental gradients are acting as environmental filters
163 for snakes, or if other processes are more important in the assembly of local communities in
164 the Pantanal and in the Paraguay River Basin.

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FINAL CONSIDERATIONS

By gathering records of snake occurrence in the Pantanal and surrounding areas and investigating the taxonomic, phylogenetic, and phenotypic diversity of communities we aimed to better understand which processes contributed and currently act to shape these communities in this floodplain. The chapters presented herein tested and originated new hypotheses that formally addressed the widely invoked theory that seasonal floods are the main ecological feature affecting biological communities in the Pantanal.

Our results about occurrence of distinct biogeographical units in the basin where the Pantanal is located showed that regarding the snake fauna, the floodplain cannot be considered a separated biogeographical region, neither was composed of regionalized faunas found in the region. Rather, the Pantanal snake fauna is part of a species group widely distributed in the study region, linked to the Paraguay River channel and nearby lowland areas. We also found evidence of a vicariant role of the Pantanal origin on the ancestral fauna of the region – the distribution of the regionalized fauna agrees with the hypothesis that some previous species ranges may have been split or limited when the floodplain arose. From these results we can infer that the present snake communities in the Pantanal were not constrained by in situ evolutionary processes, but are assemblages of species formed from a regional pool composed by faunas with diverse history and distribution. Furthermore, the Pantanal may currently act as a barrier for some species of this pool and as a dispersal corridor for others.

When we evaluated what factors drive beta diversity patterns among communities in different areas in and around the Pantanal, forest cover was the variable that explained most of the difference in composition between pairs of communities. Furthermore, beta diversity was also influenced by spatial process and climatic variables, which are important for snake physiology. Regarding the effect of seasonal floods, we found that it mainly influenced the turnover of species between assemblages. Floods seemed to be interacting

with other environmental features and could be limiting the range of some species that do not show adaptations for recurrent and seasonal flooding that bring large alterations to the environments. These results helped us to identify through which environmental features the forces that currently shape local communities in the Pantanal can be operating.

Lastly, we investigated how the phylogenetic and phenotypic structure of local communities inside and around the Pantanal were correlated with the gradient of forest cover and flood intensity. Our expectation that seasonal flooding could act as an environmental filter was not supported. For the most part, local assemblages from flooded areas were randomly structured from the regional pool and did not show morphological convergence regarding specific traits that theoretically improve the use of flooded environments. Contrarily, those communities were composed of species with morphological divergence regarding traits related to aquatic habits, while showing a higher similarity in body shape. Based on these results, we suspect that seasonal flooding, besides favoring the occurrence of aquatic species, is decreasing the relative force of deterministic processes on community assembly and can be favoring species with generalist habits by promoting recurrent ecosystem disturbances. We also provide evidence that an environmental filter can be acting through the forest cover gradient. More forested areas had lower species richness and showed morphological convergence, but they did not show lower functional diversity when compared to open areas. This means that historical divergences among the regional pool of different local communities may also have originated the observed pattern, rather than an isolated action of environmental filtering.

Overall, the present dissertation showed that the composition of snake communities in the Pantanal is influenced by seasonal flooding and by other environmental (forest cover), climatic (minimum temperature), and historical factors. Seasonal flooding seems not to act on species as an environmental filter that shape local communities in a specific way. At least for these mobile organisms, the main role of flooding is producing recurrent disturbances in

53 the ecosystems, therefore increasing the effect of random processes on the assembly of
54 communities. Furthermore, our study provided a set of new hypotheses to be addressed
55 and extended to other seasonally flooded areas, what can contribute to a better
56 understanding of the origins and maintenance of the biota in the Pantanal and other similar
57 regions.