Biodiversity from a historical geology perspective: a case study from Marajó Island, lower Amazon

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ABSTRACT

Assessing patterns of abundance and distribution of Amazonian species is still an overwhelming task that requires integration of multiple disciplines. This work is based on background information gathered from previous reconstructions of the geological history of the lower Amazon drainage basin, in order to analyse biodiversity patterns within the context of landscape transformation. A highly dynamic geological scenario is depicted for this area during the Plio-Pleistocene and Holocene, which consisted of a large palaeovalley formed as a response of tectonic reactivation. This palaeovalley was filled with sediments transported by a north/northwest orientated palaeo-Tocantins River. The palaeodrainage became abandoned as the main river course was deviated to the northeast, initiating the separation of Marajó Island from mainland. Geology had a direct impact on the modern physiognomy, with open vegetation dominating in areas with Holocene sedimentation, while closed forests prevailing in older Quaternary and, probably also, Pliocene terrains. Data from fossil and modern mammalian groups indicate the connection of Marajó Island to the mainland during the Last Glacial Maximum, when open vegetation seems to have dominated. Tectonic subsidence was responsible for the maintenance of this vegetation pattern on the eastern side of the Marajó Island, keeping it as a habitat favourable for savanna adapted faunal elements. Based on this kind of information, this work attempts to highlight the importance of integrating studies combining geological and biological events as the key to understand biodiversity patterns in Amazonia. It is expected to open new lines of research dealing with the comprehension of ecology, species and genetic diversity, biogeography, evolutionary scenarios, and speciation mechanisms.

Received 1 March 06; accepted 15 June 06

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INTRODUCTION

The Amazon drainage basin, with its associated luxurious biodiversity, is well known as the most impressive ecosystem on Earth, occupying an immense forested lowland area of 6.85 million square kilometres, over 50% of which is in Brazilian territory. A superficial and broad overview of this large area can produce the deceptive impression of a homogeneous ecosystem with an associated continuous and dense tree canopy caused, in part, by the smooth topography. Such an interpretation can be misleading when one tries to identify the natural events responsible for the origin and maintenance of such an intertwined and complex biological system. There is increasing evidence that the distribution of floristic communities within the Amazon region is rather heterogeneous (e.g. Hess et al., 2003; Lu et al., 2003) and mostly related to soil conditions (Salovaara et al., 2005).

The known levels of plant species diversity and, consequently, their animal dwellers, are far from satisfactory to furnish conclusive answers for the understanding of the factors controlling speciation events in Amazonia (Tuomisto et al., 2003). Many speciation hypotheses, however, have been built considering environmental factors resulting, either directly or indirectly, from geological processes (Rüegg & Rosenzweig, 1949; Irion, 1984; Räsänen et al., 1987, 1990, 1995; Campbell, 1990; Hoorn, 1994; Hoorn et al., 1995; Irion et al., 1995; Webb, 1995; Patton et al., 2000; Van der Hammen & Hooghiemstra, 2000; Patton & Silva, 2001; Renaud & Dam, 2002), with subsequent impacts on both the structure of the biotic components and the beta and gamma diversity patterns (Hooghiemstra & Van der Hammen, 1998). Many workers have also pointed out the importance of changes in the physical environment over the last million years as the main cause for speciation of the Amazonian biota (Absy et al., 1991; ...
der Hammen et al., 1992; Webb & Rancy, 1996; Behling & Costa, 2000; Behling & Hooghiemstra, 2000; Freitas et al., 2001; Hafler & Prance, 2001; Hafler, 2001; Pessenda et al., 2001; Sifeddine et al., 2001). However, the Amazonia is still ‘in urgent need of new geological data to provide models of landscape evolution that can serve as a foundation for discussing the origin, evolution, and the mechanisms controlling the distribution of its biodiversity’ (Rossetti et al., 2005; p. 78).

The goal of this paper is to highlight the importance of introducing geological data into studies focusing on the analysis of the Amazonian biodiversity. The lower Amazon drainage system, in great part represented by the Marajó Island, seems to be appropriate for advancing in this discussion, given that it contains a large area of late Tertiary to Holocene geological units. Deposits of these ages are very attractive for studies concerning the biodiversity because this time interval witnessed the explosion of most of the modern tropical species (e.g. Patton & Silva, 2001; Richardson et al., 2001). A recent regional study emphasizing the geological evolution of Amazonian areas has highlighted its high dynamism in a relatively recent time (Rossetti et al., 2005), which makes it of special interest to test the impact of geologically driven environmental changes on both rates and mode of speciation. Although further studies must be undertaken before the relationship between abiotic and biotic processes can be better understood, there is an urgent need in providing preliminary models to discuss the main factors that might have contributed for the establishment of the high levels of Amazonian biodiversity.

GENERAL PHYSIOGRAPHY OF THE STUDY AREA

The lower Amazon drainage basin is formed by two main rivers, the Amazon and the Tocantins, in the west and the east of the Marajó Island, respectively (Fig. 1). The first gradually changes its downstream orientation from east/northeast to northeast, branching near the vicinity of the town of Almerim. From there, a landscape dominated by many islands of variable sizes extends through a distance greater than about 400 km, up to the point of discharge into the Atlantic Ocean.

The lower courses of the Amazon–Tocantins basin are located in a region of tropical climate characterized by mean annual temperature of 28 °C and precipitation of 2500–3000 mm year⁻¹, 90% of which are concentrated between January and July. The low topographical terrain, usually < 25–30 m a.s.l. in most of the area, is surrounded by higher lands consisting of pre-Cambrian rocks of the Guiana Shield to the northwest; Cretaceous rocks of the Alter do Chão Formation to the west and southwest; pre-Cambrian rocks of the Brazil Central Shield and Cretaceous rocks of the Grajau Basin to the south and southeast; and Cretaceous rocks of the Itacurubí Group and late Tertiary deposits of the Pirabas/Barreiras Formations to the east and northeast (Fig. 1). These deposits are truncated by younger, Plio-Pleistocene and Holocene strata, mostly represented by sands referred to generically as the Post-Barreiras Sediments (Rossetti, 2004). It is interesting to note that, in general, an open vegetation pattern dominates in areas with Holocene sedimentation, while ombrophyla forests are widespread on older deposits.

APPROACHING BIODIVERSITY DISTRIBUTION IN THE MARAJÓ ISLAND

The origin of the Amazonian biodiversity is a complex issue that might have different controls if distinct taxonomic groups are considered (Patton & Silva, 2001, 2005; Tuomisto et al., 2003). In general, there are two models attempting to explain biodiversity changes through time: (i) each species responds independently to changes in either physical environments or biological components in order to meet its specific physiological needs (Gleason, 1926); and (ii) communities change as broader and intact biogeographical units in response to environmental variations (Clemens, 1916). Both ecological patterns, which can be identified in the fossil record (Lyons, 2005), represent effective adaptive strategies in maintaining the production of offspring and avoiding extinction, and should be considered under more comprehensive conservation studies.

This paper highlights the importance of environmental control linked to geological changes on the development of the Amazonian biodiversity. Many theories aiming to explain the origin of this biodiversity have been founded directly or indirectly on geological information (e.g. Rüegg & Rosenzweig, 1949; Räsänen et al., 1995; Webb, 1995; Patton et al., 2000; Bates, 2001; Patton & Silva, 2001). These are, though, still highly speculative due to the overall lack of detailed geological information available from this area (e.g. Van der Hammen & Hooghiemstra, 2000). In particular, landscape development since the Miocene, and the driving mechanisms, remains to be discussed based on a larger volume of geological information.

A dynamic geological scenario during Plio-Pleistocene to Holocene times

Our recent study combining geological and geomorphological data, presented in a separate work recently submitted for publication, has shown that the lower Amazon drainage area experienced substantial modification in its physiography after the Miocene. These changes, which might have taken place even during the Holocene, were dictated by fault displacements, which affected the landscape by imposing reorientations on drainage systems, creation of new river courses, and development of different distributions between flooded and nonflooded areas (Costa et al., 1996; Costa & Hasui, 1997).

As a brief summary, a general picture of the lower Amazon drainage area considers the existence of a tectonically controlled north/northwest and south/southeast-orientated palaeovalley cut down into Miocene and older rocks. The incised valley was fed by a palaeo-Tocantins River, which deposited its sediment
load continuously to the north/northwest, reaching Marajó Island and producing a deposit with a funnel morphology during the Plio-Pleistocene/Pleistocene (Fig. 1). Numerous abandoned channels, which are associated with deposits of this age on the western side of this island, are regarded as the record of this palaeodrainage system.

Following the Plio-Pleistocene, the palaeo-Tocantins River became abandoned, as its main course was captured by northeast/southwest orientated faults, which initiated the fragmentation of the Marajo area from mainland. East-west strike-slip faults developed during the Holocene would have led to the establishment of the Pará River, a process that gave rise to an east/northeast orientated segment in the lower Tocantins River. As a result, the Marajó Island was finally detached from the mainland. Shortly before, a large part of the eastern side of the island subsided, with only a narrow belt, consisting of Plio-Pleistocene and Miocene deposits, remaining stable in its easternmost edge. Subsidence took place probably in early Holocene, as suggested by frequent sedimentary strata as young as up to 6990 (+/60) $^{14}$C year BP (Rossetti, unpublished data) in the eastern side of the island, which have not been recorded to the west. In addition to the presence of many structural lineaments (e.g. Bemerguy, 1997), the concentration of several NW–SE tectonic traces at the boundary of the two physiographic compartments of the island suggests a tectonic control of the subsidence. Hence, the eastern part of the island was
s slightly depressed tectonically relatively to the western side, a process that would have promoted the creation of new space (only a few metres) to accommodate a middle to late Holocene sedimentation.

The geological history synthesized above is, therefore, consistent with a highly dynamic scenario for the lower Amazon drainage system during Plio-Pleistocene/Holocene times. It is unquestionable from the available information that tectonic reactivations had a very important contribution to the development of the physical environments and renewal of sediment deposition in the study area during the Quaternary. In addition to tectonics, one cannot discard the possibility that the return to sediment deposition in the eastern compartment of the Marajó Island might have been also influenced by the Holocene transgression and high stand, a hypothesis that deserves to be further investigated.

**Impacts to biodiversity analysis**

The impact of a dynamic environmental evolution on the associated biota remains to be deciphered. The construction of models to explain both rates and mode of speciation is certainly a complex issue that deserves further efforts undertaken in a cooperative and multidisciplinary basis. To initiate this process, however, the following discussion aims to demonstrate how such a scenario, dominated by highly unstable environmental conditions, might have defined some patterns of species distribution observed in the Marajó Island.

In the absence of further data, modelling the distribution of species and communities can be approached using vegetation types (Crowling et al., 2001; Foody, 2003; Kerr & Ostrovsky, 2003). For the particular case of the study area, regardless of the homogeneous climate, it is noteworthy that there is a sharp contrast in vegetation patterns between deposits formed within different geological contexts within the Plio-Pleistocene/Holocene palaeovalley. This is well illustrated in the Marajó Island (Fig. 2A–D), where a uniform and dense ombrophyla vegetation prevails to the west in terrains composed by Plio-Pleistocene sediments, in contrast to Holocene areas to the east, dominated by open vegetation. The latter includes mostly treeless grasslands (*campo*) and savanna woodlands (sense Furley, 1999), as well as several elongated and sinuous belts of arboreal vegetation associated with the remains of sandy palaeochannels. In the easternmost side of the island, there is also a narrow belt of dense canopy developed in relatively higher lands dominated by Pleistocene and Miocene deposits.

Considering the uniform climate, the sharp contrast in vegetation styles observed in Marajó Island is highly intriguing. It has been proposed that open vegetation located in tropical forest areas might be the record of past Holocene drier climates (Ledru, 2002; Ledru et al., 2006). In particular, these authors have stated that the first appearance of *cerrados* in Amazonia took place 10 000 years BP as a result of progressive increase in seasonality, and that their presence in the modern setting evidences a past connection with central Brazilian areas during extreme climatic conditions.

The existence of alternating wet and dry periods in Amazonia during the late Quaternary, with the consequent mobility between forests and savannas, has been a matter of great debate among specialists of several disciplines (e.g. Räsänen et al., 1990; Van der Hammen et al., 1992; Latrubesse & Rancy, 1998; Hafler, 2001; Mörner et al., 2001; Siefeddine et al., 2001; Van der Hammen, 2001; Ruter et al., 2004). In particular, pollen data from Amazonian areas have attested periods drier than today’s (Behling & Hooghiemstra, 1999; Behling et al., 1999, 2001; Behling & Costa, 2000, 2001; Mayle et al., 2000; Baker et al., 2001; Freitas et al., 2001; Pessenda et al., 2004), with development of open vegetation at least two times during the Last Glacial Maximum predict the existence of savanna vegetation in northeastern Amazonia, caused by the occurrence of dry seasons twice as long as today’s, when rainfalls were decreased to 25–35% (Vizy & Cook, 2005; Cook & Vizy, 2006). In addition, the expansion of open vegetation in northeastern Amazonia during the Younger Dryas is in agreement with a proposed decrease of, at least, 40% of river discharge (Maslin & Burns, 2000). Only in the mid-Holocene does there seem to have been a change to wetter climates (Ruter et al., 2004).

For the case of Marajó Island, there have been no efforts aiming to demonstrate the presence of open vegetation during the Late Quaternary, neither to explain how these areas could have remained stable up to the present within a tropical forest environment. However, some interesting palaeoecological information supporting latest Quaternary environmental changes in this area is worthy of citation. The first is the documentation of remains of the mastodont species *Haplomastodon waringi* on Marajó Island (Simpson & Paula Couto, 1957). Similar fossils recorded in a central Amazonian area, that is, in the adjacency of the town of Itaituba, PA, displayed an AMS radiocarbon age of only 15 290 (± 70) 14C year BP (Rossetti et al., 2004). The mastodont-bearing stratigraphic horizon from that area is overlain by another fossiliferous deposit containing an *in situ* community of *Eremotherium laurillardi*, dated at 11 340 (± 50) 14C year BP. These records suggest that the modern dense canopy developed not long ago. These species are common in several other Brazilian sites, which has been used to support the existence of open habitats during the Late Cenozoic in northern South America (Rancy, 1991, 2000; Cartelle, 1999; Vivo & Carmignotto, 2004). The occurrence of mastodont remains on Marajó Island implies the existence of a former connection with mainland areas having an open vegetation structure.

A second source of palaeoecological information is provided by the occurrence in the paleofauna of the cervid species *Ozotocerus bezoaerticus* in the Serra dos Carajás region, southern portion of the State of Pará, at around 8000–2000 year BP (Toledo et al., 1999). This *pampas* deer is an animal of open
vegetation from central and southern South America between the latitudes of 5–45°S (Fig. 3). This faunal element has also been recorded in historical times in most of the natural grasslands below the Equator. (Eisenberg & Redford, 1999; González et al., 2002). Recent ongoing studies have recorded this cervid living in natural populations in the areas with open vegetation located in the south-eastern side of the Marajó Island (J. da Silva Junior, pers. comm.). Its unexpected presence conforms to the existence of a continuous connection between this island and open terrestrial environments of central and...
southern Brazil, from where the deer could have derived during the relatively recent past (i.e. Holocene) times.

Based on the above discussion, it seems likely that the Marajó Island and, likewise many other Amazonian areas, was affected by early Holocene drier climates, favouring the development of large areas dominated by open vegetation. However, the maintenance of these areas on the eastern side of the island, rather than having a climatic control, appears to be linked to a geological context (i.e. subsidence, possibly combined with relative sea level rise, followed by renewed sediment deposition), which created an environment favourable for maintaining a predominantly open vegetation style suitable to the deer’s habitat requirements.

Although a full characterization of vegetation types in the study area is beyond the scope of this work, a general model applied to the geological history proposed above might be suggested to explain the overall bipartite vegetation pattern observed in the Marajó Island. Hence, subsidence due to tectonic reactivation was responsible for creation of new space to accommodate sediments in the eastern side of the island in more recent (i.e. mid- to late Holocene) times, a process that might have been combined with a concurrent rise in relative sea level. As a consequence, these areas have been undergone continued sedimentation, with no time for a dense vegetation to develop. In addition to time, subsidence brought this area down to the water table level, positioned only a few metres below the surface, precluding large root fixation. In contrast, as the climate became progressively wetter from the mid-Holocene, older (i.e. Miocene to Pleistocene) terrains that remained relatively more stable in the west of Marajó Island, as well as along a narrow belt in its easternmost edge, became a locus favourable for colonization of an arboreal vegetation.

It is interesting to note that, as the eastern side of the island has become more stable and filled with sediments, some areas characterized by open vegetation appear to have been progressively replaced by arboreal vegetation. This is illustrated by the palaeochannels, which have remained stable for a longer period of time and are topographically slightly higher (thus more protected from seasonal floodings) relatively to surrounding open areas. These characteristics resulted in sites more favourable for tree growth, with the consequent development of the belts of vegetation that are typically highly sinuous and elongated in the eastern side of Marajó Island.

**CONCLUDING REMARKS**

There is a growing consensus among biologists on the advantages of using multiple data sets provided by different fields of research for discussing modes of speciation. Although a clear linkage between ecosystem functioning and levels of species diversity has not been presented yet (Lawler et al., 2002; references therein), new evidence has gradually been gathered to test such proposed relationships. The effective advances in our knowledge of speciation events in Amazonia require an additional comprehensive understanding of causal factors, considering the integration of both abiotic and biotic studies.

In this regard, research agendas focusing on the historical and causal factors responsible for generation and development of modern habitats may become a useful tool to help accomplish such an endeavour.

New developments on climate and climate modelling (e.g. Botta et al., 2002; Ruter et al., 2004; Vizy & Cook, 2005; Cook & Vizy, 2006) have provided important elements for helping reconstructing past landscapes. However, as stated by Margules & Austin (1995), there is still an urgent need to create a larger database to adequately record the biota regarding the establishment of recent and past geographical ranges, helping towards the formulation of robust biological models for monitoring and predicting species decline. The integration of biodiversity patterns with both geological and fossil data provide the necessary background for the understanding of current biological interactions. In this context, the essay provided for the Marajó Island might serve to motive new interdisciplinary projects aiming to understand the occurrence of open vegetation patterns within tropical rainforest areas. Despite the possible influence of past climates, the maintenance of a savanna-like
environment in the eastern side of this island seems to have been linked to a dynamic geological evolution of the physical environment. This was caused by a slight tectonic subsidence, a process that would have favoured submergence and renewed sediment deposition. As a result of seasonal floodings, this Holocene lowland area is still submerged during a considerable time of the year, precluding tree growth, as opposed to older, more stable and slightly higher terrains located to the west of the island and along the narrow belt in its easternmost edge.

Therefore, temporal and spatial scales are of fundamental significance for interpreting and understanding biogeography and community structure patterns in order to establish the basis to undertake research projects aiming to discuss biodiversity events and strategies for species conservation. The presentation of feasible and coherent proposals that might help to understand the controlling mechanisms involved in species evolution, as well as prevent their extinctions, should be based on a multidisciplinary approach including: (i) geological history, (ii) ecological field studies, (iii) knowledge of broad biogeographical patterns, and (iv) control of species climatic tolerance requirements.

ACKNOWLEDGEMENTS

The authors want to acknowledge the financial support provided by FAPESP (Project no. 004/15518-6). Dr H. Gregory McDonald is thanked for the critical review of the manuscript. The researcher from the Goeldi Museum Dr José da Silva Junior contributed with discussion on the matter of modern Amazonian mammalian biogeography. The authors also thank two anonymous reviewers who helped with many comments and suggestions that have contributed to significantly improve the manuscript.

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