

**INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA**

**Dinâmica Espacial da Assembleia de Mamíferos de Médio e Grande
Portes em Ambientes de Várzea e Terra Firme na Amazônia
Central**

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**Dinâmica Espacial da Assembleia de Mamíferos de Médio e Grande Portes
em Ambientes de Várzea e Terra Firme na Amazônia Central**

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PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

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Aos 16 dias do mês de maio do ano de 2017, às 14h00min, no Auditório do LBA, Campus II, INPA/Aleixo. Reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Rafael do Nascimento Leite**, do Instituto Nacional de Pesquisas da Amazônia - INPA, o(a) Prof(a). Dr(a). **Adrian Paul Ashton Barnett**, do Instituto Nacional de Pesquisas da Amazônia - INPA, e o(a) Prof(a). Dr(a). **Marcelo Gordo**, da Universidade Federal do Amazonas - UFAM, tendo como suplentes o(a) Prof(a). Dr(a). Rafael Leandro de Assis, do Instituto Nacional de Pesquisas da Amazônia - INPA, e o(a) Prof(a). Dr(a). José Luís Campana Camargo, do Instituto Nacional de Pesquisas da Amazônia, sob a presidência do(a) primeiro(a), a fim de proceder a arguição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **GUILHERME COSTA ALVARENGA**, intitulado: "**DINÂMICA ESPACIAL DA ASSEMBLEIA DE MAMÍFEROS DE MÉDIO E GRANDE PORTES EM AMBIENTES DE VÁRZEA E TERRA FIRME NA AMAZÔNIA CENTRAL**", orientado(a) pelo(a) Prof(a). Dr(a). Paulo Estefano Dineli Bobrowiec, do Instituto Nacional de Pesquisas da Amazônia - INPA, e coorientado(a) pelo(a) Prof(a). Dr(a). Emiliano Esterci Ramalho, do Instituto de Desenvolvimento Sustentável Mamirauá - IDSM, e pelo(a) Prof(a). Dr(a). Fabrício Beggiano Baccaro, da Universidade Federal do Amazonas - UFAM.

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Sinopse:

Avaliamos como os tipos de vegetação influenciam a composição e distribuição das espécies de mamíferos terrestres de médio e grande portes durante a seca. A composição de espécies foi diferente entre as florestas de várzea e de terra firme. Especificamente, na floresta de várzea as diferentes fitofisionomias influenciaram a distribuição dos mamíferos. No geral, mamíferos de médio porte evitaram habitats que permanecem mais tempo alagados, enquanto a onça pintada parecer usar mais frequentemente as zonas de transição entre ambientes aquático e terrestres.

Palavras-chave: Ecologia de mamíferos, Florestas de várzea e terra firme - Amazônia, armadilhas fotográficas.

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“A crise ambiental não pode ser resolvida apenas pela ciência e pela política. Ela é um tema moral, determinado por cultura e caráter. Nós precisamos de uma mudança de atitude, de consciência, de prioridades e de expectativas, uma nova estratégia para a sobrevivência humana, que condena o desperdício e a destruição, e que coloca um valor espiritual em cuidar bem do mundo natural.”

George Schaller

Resumo

Entender o uso do espaço por mamíferos é extremamente importante para tomada de decisões eficazes para conservação. Na Amazônia, apesar deste grupo ser intensamente estudado, pouco se sabe sobre sua relação com as florestas de várzea. As florestas de várzea estão restritas às planícies inundáveis nas calhas dos grandes rios de água branca. Essas florestas foram, e ainda são, intensamente utilizadas pelo homem, devido ao fácil acesso e aos solos férteis. Além disso, as mudanças climáticas e as políticas de incentivo à produção energética via barragens hidrelétricas são ameaças diretas às florestas inundáveis e à fauna associada. Com intuito de melhor entender a distribuição das espécies de mamíferos de médio e grande portes na várzea, executamos dois anos consecutivos de amostragem durante a estação seca nas RDS's Amanã e Mamirauá, Amazônia Central. Comparamos a comunidade das espécies de mamíferos entre terra firme (RDSA) e várzea (RDSM), e testamos a influência das fitofisionomias da várzea na distribuição das espécies de mamíferos lá registradas. A grade de amostragem em cada RDS consistiu de 50 estações com um par de armadilhas fotográficas iscadas. O esforço de campo total foi de 4075 armadilhas fotográficas*dia. A partir do mapeamento espacial pré-existente da RDSM nós determinamos duas escalas de buffer com raio de 500 m e 1000 m ao redor das estações fotográficas e mensuramos a área ocupada (km²) por cada classe de habitat. Para comparação entre as comunidades de mamíferos da terra firme e da várzea usamos uma ordenação por NMDS de duas dimensões e em seguida uma Análise de Similaridade (ANOSIM), ambos baseados no índice de similaridade de Bray-Curtis. Para testar a influência das fitofisionomias da várzea na distribuição dos mamíferos usamos Modelos Lineares Generalizados (GLM) e, para espécies com excesso de zeros, modelos de Zeros-Inflados (ZIP/ZINB) e modelos de Obstáculo (ZAP/ZANB). Nós registramos 21 espécies de mamíferos de médio e grande portes de um total de 3443 registros. Dentre as espécies registradas, sete são classificadas como 'vulneráveis' globalmente ou em listas do Brasil. Como esperado as comunidades de mamíferos foram dissimilares entre várzea e terra firme. Na várzea foram registradas apenas seis espécies, enquanto na terra firme foram 20 espécies. A comunidade de mamíferos da floresta de várzea apresentou um padrão de subgrupo hierárquico da comunidade da terra firme, sendo que todas as espécies registradas na várzea possuem hábitos semi-arborícolas. Das cinco espécies compartilhadas entre os dois ambientes, três espécies foram registradas com maior frequência na várzea, o que pode estar relacionado com maiores populações nesses ambientes. As fitofisionomias da várzea influenciaram a distribuição de todos os mamíferos testados, com exceção de *Leopardus wiedii*. O número total de registros e a composição das espécies foram influenciados pelo chavascal, sendo que houveram menos registros com aumento da área de chavascal. Do mesmo modo, *Didelphis marsupialis* e *Nasua nasua* também evitaram o chavascal. *N. nasua* também foi menos registrada nos campos abertos de vegetação herbácea. A espécie *Coendou prehensilis* teve relação positiva com os habitats água constante e várzea alta, enquanto *Panthera onca* evitou a várzea alta. Este é o primeiro estudo de comunidade de mamíferos com foco em ambientes de várzea, portanto novos estudos são necessários para se entender os padrões em outras regiões de várzea, o que auxiliará diretamente no direcionamento de ações conservacionistas.

Abstract

Title: Spatial dynamics of medium- and large-sized mammal assemblages in várzea and terra firme forests, Central Amazonia, Brazil

Studies that try to understand how mammals use the space are extremely important to improve conservation decisions. Despite the high knowledge of mammals in the Amazon forest, little is known about this group in the varzea forests. These forests are located in the lowland inundated regions of the Amazon basin, and are seasonally inundated by white-water rivers. Varzea forests were, and still are, intensively used by humans, because of the easy access and the high fertility of its soils. Beyond that, climatic changes and the actual Brazilian politics, which encourages constructions of hydroelectric plants, are direct threats to the varzea and the animals that live there. The goal of this study is to understand how variations in the vegetation influence the distribution of medium and large-sized mammals in the varzea forest. For this, we executed two consecutive years of camera trap surveys during dry season in Sustainable Development Reserves Amanã and Mamirauá, Central Amazonia. Specifically, we compared the community composition of mammals between an upland forest (Amanã) and a varzea forest (Mamirauá), and we tested the response of mammal species to the vegetation variation in the varzea forest. The sampling grid in each reserve consisted of up to 50 baited camera trap stations and an overall sampling effort of 4075 camera trap*days. We used a pre-existing landscape mapping of Mamirauá Reserve and from it we calculated the area (km²) of the habitats inside two different scales (500 m and 1000 m) around each camera trap station. The comparison between the mammal species of upland and varzea was made with an ordination by NMDS of two dimensions and after that a Similarity Analysis (ANOSIM), both using Bray-Curtis indices. To test the influence of the varzea vegetation on the mammal distribution we used Generalized Linear Models (GLM) and, for the species with too many zeros, Zero-Inflated Models (ZIP/ZINB) or Hurdle Models (ZAP/ZANB). During the study, we recorded 21 medium and large-sized mammal species of 3443 records. Among these species, seven are classified as 'vulnerable' globally or in Brazil. As expected the community composition of mammals was different between upland and varzea forest. At the varzea we recorded only six species, while upland recorded 20 species. The mammal community of varzea forest presented a hierarchical subgroup pattern of the upland community, and all the species registered in the varzea have semi-arboreal habits. Tree species recorded in varzea forest were more represented there than in upland forest, which could be related with biggest populations at this region. The varzea vegetation was related with almost all species distributions, the exception was *Leopardus wiedii*. The total number of records and the composition of species were influenced by the habitat chavascal, such that there were fewer records with chavascal area increase. At the same way, *Didelphis marsupialis* e *Nasua nasua* avoided areas of chavascal. *N. nasua* avoided too the open fields of herbaceous vegetation. The species *Coendou prehensilis* was positively influenced by constant water habitats and high varzea forest, while *Panthera onca* avoided high varzea forest.

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Introdução Geral

A floresta Amazônica cobre uma área aproximada de 7 milhões de hectares, é a maior floresta tropical contínua do mundo e abriga uma parte importante da biodiversidade global. Esta vasta região possui diferentes tipos de solo que associados à variedade de rios existentes formam um mosaico de paisagens dominado por florestas de terra firme entremeados por diversos habitats alagáveis (Hess et al. 2003, Junk et al. 2011, Quesada et al. 2011). Os picos de frutificação nas diferentes formações florestais nem sempre ocorrem na mesma estação (Haugaasen & Peres, 2007), de modo que em regiões de transição entre florestas inundáveis e não-inundáveis, esta assincronicidade possibilita a manutenção da diversidade local que pode se deslocar no espaço em resposta à disponibilidade dos recursos (Voss & Emmons 1996, Haugaasen & Peres, 2007). Por outro lado, as variações sazonais nos ambientes inundáveis são restritivas para grande parte das espécies que não possuem caracteres adaptados para sobreviver à inundaçãõ.

As áreas inundáveis representam 14% da bacia amazônica e sua dinâmica é regida principalmente pela intensidade e duração da inundaçãõ, assim como pela composição físico-química dos rios associados (Hess et al. 2015, Junk et al. 2015). Dentre os 14% de habitats alagáveis, as florestas de várzea são as mais extensas, cobrindo metade desta área, com aproximadamente 300.000 km² (Melack and Hess 2010). Estas florestas são alagadas por rios de água barrenta com alta concentração de nutrientes provenientes do degelo dos Andes (Prance 1979). Devido ao constante aporte de nutrientes, as florestas de várzea têm a maior produtividade primária da Amazônia, sendo três vezes maior que na terra firme (Schöngart et al. 2010). Os pulsos de inundaçãõ na várzea são monomodais e sua intensidade é um fator limitante para as espécies de árvores, de modo que diversas estratégias adaptativas foram selecionadas para possibilitar a sobrevivência nesse ambiente. Dentre essas estratégias são destacadas a presença de raízes adventícias e lenticelas que maximizam a aeração das raízes

(Parolin 2001) e a dispersão de frutos e sementes pela água (hidrocoria) e pelos peixes (ictiocoria) nos períodos inundados (Gottsberger 1978, Junk et al. 1989, Kubitzki and Ziburski 1994, Lopez 2001). Conseqüentemente, o tempo de inundação e a topografia na várzea resultam na formação de três principais formações florestais (Ayres 1993, Wittmann et al. 2002, Junk et al. 2012): (1) chavascal, áreas baixas com solos permanentemente encharcados, caracterizado por dossel baixo, dominado por lianas e com menos espécies de árvores comparado com as outras fitofisionomias; (2) várzea baixa com níveis de alagamento acima de 3 m e duração superior a 90 dias/ano, formado por espécies arbóreas adaptadas a alagamentos prolongados, de modo a ter apenas 10% de espécies similares com a terra firme; (3) várzea alta, região de transição entre áreas alagadas e não alagadas, com nível da água menor que 3 m e a duração inferior a 90 dias/ano, a formação arbórea é mais semelhante às florestas de terra firme, compartilhando em torno de 30% das espécies.

A terra firme, por outro lado, nunca fica inundada, o que favorece a ocorrência de um maior número de espécies da flora (Junk et al. 1989, Ayres 1993, Haugaasen and Peres 2006). Sua formação geológica é dividida em dois momentos, sedimentos mais antigos, depositados no terciário, e sedimentos mais recentes, depositados no pleistoceno, também conhecidos como paleovárzeas (Irion et al. 2010). Apesar dos solos da paleovárzea terem mais nutrientes que os solos formados no terciário, ambos são considerados solos pobres quando comparados à várzea (Junk et al. 2012). Como os solos de terra firme não são inundados, a entrada de nutrientes no solo é menor (Irion et al. 1997), o que favoreceu estratégias que maximizam a captação dos nutrientes pelas plantas (Luizão and Schubart 1987), além de outras adaptações como a redução da perda de estruturas energeticamente custosas, como as folhas (Haugaasen and Peres 2005a). Conseqüentemente, a produção de frutos da terra firme é aparentemente menor

que na várzea (Ayres 1993, Peres 1994, 1997). A diferença entre produtividade e composição da flora podem influenciar a distribuição e abundância das espécies animais.

A diferença na composição das espécies de mamíferos entre florestas de várzea e terra firme tem sido demonstrada para vários táxons, como morcegos (Pereira et al. 2009; Bobrowiec et al. 2014), primatas (Branch 1983; Peres 1997; Haugaasen & Peres 2007) e mamíferos de médio e grande portes (Bodmer 1990; Haugaasen & Peres 2005b). Para as espécies exclusivamente terrestres, a inundação sazonal é um fator limitante para a sua distribuição, pois diminui a área de terra disponível. Diversos estudos têm demonstrado um fluxo sazonal de algumas espécies entre a várzea e a terra firme contígua, no qual as espécies migram durante a vazante para a várzea em busca de alimento, como frutos, sementes e brotos, retornando para a terra firme durante as cheias (Bodmer 1990; Haugaasen & Peres 2005b, 2007).

Áreas com relevo mais alto também podem influenciar a dinâmica de movimentação e ocupação da várzea por mamíferos terrestres, onde ilhas não submersas podem ser usadas como local de alimentação e descanso durante o período de cheia (Bodmer 1990, Fragoso 1998). Esta característica do relevo favorece espécies de animais terrestres com alta capacidade de dispersão e habilidade natatória, como queixadas (*Tayassu pecari*) e antas (*Tapirus terrestris*) (Medici 2010). Estas espécies podem nadar entre as ilhas a procura de alimento e abrigo, podendo até aumentar sua área de vida durante o período de cheia (Fragoso 1998). Estudos que avaliaram a estrutura das assembleias de mamíferos terrestres em ambientes periodicamente alagáveis usaram principalmente transectos lineares como técnica para inventariar as espécies (Haugaasen and Peres 2005b, 2007). Por outro lado, o armadilhamento fotográfico é um método amplamente reconhecido pela qualidade dos registros,

possibilitando maior eficiência na identificação das espécies e na captura de espécies elusivas (e. g. Rocha et al. 2015). Dessa maneira, o objetivo deste estudo foi entender como os tipos de vegetação influenciam a composição e distribuição das espécies de mamíferos terrestres de médio e grande portes durante a seca, através do armadilhamento fotográfico.

Objetivos

1. Estimar a similaridade da composição de espécies de mamíferos de médio e grande portes entre uma floresta de várzea e uma floresta de terra firme.
2. Analisar como a assembleia de mamíferos da várzea responde às variações da estrutura da vegetação das florestas de várzea.

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Spatial dynamics of medium- and large-sized mammal assemblages in várzea and terra firme forests, Central Amazonia, Brazil

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Abstract

The Amazon forest is the largest continuous tropical forest in the world, occupying an area of 7 million hectares. The mammals inhabiting this environment are not homogeneously distributed across the landscape; different biotic and abiotic factors influence and determine their presence. The goal of this study was understand how different vegetation types influence the composition and distribution of medium- and large-sized mammal's species during dry season. Specifically, we: (1) compared the species composition between a terra firme (Amanã Sustainable Development Reserve) and a várzea forest (Mamirauá); and (2) tested whether the number of records and species-composition of mammal assemblages were influenced by vegetation types in várzea. The sampling grid in each reserve consisted of up to 50 baited camera trap stations, with an overall sampling effort of 5015 camera traps*days. In várzea forest, we defined two buffer scales (500 m e 1000 m) around the camera trap stations and measured the occupied area of vegetation type. We recorded 21 medium- and large-sized mammal species in 3443 records. As expected, composition of the mammalian assemblages differed between terra firme and várzea forests. In várzea we recorded only six species, while in terra firme 20 species was recorded. Mammal assemblage in várzea forest was a subset of the terra firme mammal assemblage, and all species registered in várzea have semi-arboreal habits. In general, medium-sized mammals avoided habitats associated with long flooding periods, while *Panthera onca* appears to prefer aquatic/terrestrial transition zones.

Key words: Amazon forest; assemblage structure; mammals distribution; flooded forest; unflooded forest.

Introduction

Amazon rainforest is the world's largest continuous rainforest, covering an area of 7 million hectares and sheltering 51 species of medium- and large-sized terrestrial mammals in Brazil alone (Paglia et al. 2012). Despite its extension, the Amazon forest is increasingly threatened by different anthropogenic pressures (Fearnside 2005; Bernard et al. 2014; Lees et al. 2016). In this immense forest, the different soil types associated with the variety of lentic and lotic environments form a mosaic of landscapes dominated by terra firme forests surrounded by diverse floodable habitats (Hess et al. 2003; Junk et al. 2011; Quesada et al. 2011). Therefore, understanding how species are distributed in the available landscapes is crucial for defining effective conservation areas (McKnight et al. 2007).

Seasonally flooded environments fringing white-water rivers (locally and scientifically known as várzeas) cover an area of approximately 300,000 km² of the Amazon basin (Melack and Hess 2010). These rivers have sediment-rich waters with high concentrations of nutrients derived from Andean foothills. They are deposited annually on the floodplain soils during flood periods (Prance 1979; Junk et al. 2011) and associated with topography, these factors drive plant communities structure and diversity patterns (Wittmann et al. 2002; Junk et al. 2011; Luize et al. 2015). On the other hand, upland forests (hereafter 'terra firme' forests) rarely flood and so have lower annual nutrient inputs into the soil (Irion et al. 1997). The differences in várzea and terra firme forest productivity and its relation to the composition of the flora also influence the distribution and structure of the animal species assemblages (Janson and Emmons 1990; Peres 1999; Haugaasen and Peres 2005).

The difference in mammal species composition assemblages between seasonally-flooded forests and terra firme has been reported for several taxa, including bats (Pereira et al. 2009; Bobrowiec et al. 2014), primates (Branch 1983; Peres 1997;

Haugaasen and Peres 2009) and medium- and large-sized mammals (Bodmer 1990; Haugaasen and Peres 2005; Salvador et al. 2011). For exclusively terrestrial species, seasonal flooding is a limiting factor, as it decreases the available land area during floods. A number of studies have found seasonal movements of species between várzea and contiguous terra firme forests, in which, during the low-water season, species migrate to várzea in search of food, such as fruits, seeds and shoots, returning to the terra firme when inundation commences (Bodmer 1990; Haugaasen and Peres 2007; Salvador et al. 2011; Bobrowiec et al. 2014).

Locally, topography also influences movement and occupation dynamics of terrestrial mammals (Polisar et al. 2008; Paredes et al. 2017). During floods, higher areas may form islands in the floodplain which can be used as feeding and resting places during the flooding season, especially by species with good swimming capacity or semi-arboreal species that may move between islands (Bodmer 1990; Salvador et al. 2011). In the dry season, different floodplain vegetation types should better explain the distribution of terrestrial mammal species, since they have different structure and composition characteristics (Ayres 1993; Assis and Wittmann 2011). However, little is still known about how vegetation types influences terrestrial mammal distributions during the várzea non-flooded period. Only two studies evaluated differential use of várzea vegetation by terrestrial mammals, the first one with arboreal folivore mammals (Queiroz 1995), and the second one found a preference by *Panthera onca* for swamp areas, locally known as Chavascal (Ramalho and Magnusson 2008).

Currently, flooded forests are the most threatened environments in the Amazon basin, suffering a variety of anthropogenic pressures, such as pollution, overharvesting, deforestation for pasture-based farming and hydroelectric dam constructions (Junk 2002; Castello et al. 2013; Lees et al. 2016). Besides, the historical distribution of

humans in the Amazon forest is closely related to the great rivers. These areas historically provide resources for housing, cultivation, fishing and hunting (Junk and Piedade 2010; Clement et al. 2015; Antunes et al. 2016). The present study aimed to understand how vegetation types influence the composition and distribution of medium- and large-sized terrestrial mammals during low-water season in terra-firme and seasonally flooded forests (várzea forests). Specifically, we: (1) compared the similarity of the mammalian assemblage in a continuous terra firme forest and a várzea forest isolated between two large rivers (Amazonas and Japurá), and (2) evaluated how mammal assemblage respond to different várzea forest types. We predict that mammalian assemblage composition in várzea forest will be a subset of the terra-firme forest diversity. Both environments are strikingly different from each other, but the flood pulse in the lowland varzea forest is probably the main driver separating mammalian assemblages composition, once just a few number of species living in terra firme forest are capable to adapt to a half-year flooded life. We also expect that floodplain species will be recorded more frequently in forests flooded for shorter periods (high várzea). These environments remain dry for longer periods, allowing greater movement of species via unflooded forest floor, besides they have higher biomass and number of species, and consequently, greater supply of food (Ayres 1993; Assis and Wittmann 2011).

Methods

Study area

Fieldwork was carried out in Mamirauá (MSDR) and Amanã (ASDR) Sustainable Development Reserves, both located in Central Amazonia, in the state of Amazonas, Brazil (Fig. 1). The climate in the region is tropical humid, with average

temperature of 29.5°C and 2373 mm rainfall (Ayres 1993). The driest period occurs between July and October, and the wettest period between December and March (Ayres 1993).

MSDR (1°49' to 3°09' S, 64°45' to 67°23' W) is delimited by the Amazonas and Japurá rivers and encompasses an area of 1,124,000 ha entirely composed by floodplain environments, being the largest area devoted exclusively to protecting floodplain forests in the Amazon. Seasons are divided between flooded (May to July) and non-flooded (September to November) periods, related with the rise and fall of the waters (Ramalho et al. 2009). ASDR (2°21'S, 64°16'W) lies in the interfluvium between the Japura and Negro rivers and cover an area of 2,350,000 ha. Along with Jaú National Park and MSDR, the three protected areas form the Central Amazon Corridor, a conservation zone of 5,746,000 ha. The ASDR it is mainly composed by unflooded terra firme forests, so that annual floods are limited to the banks of narrower floodplains (Queiroz 2005).

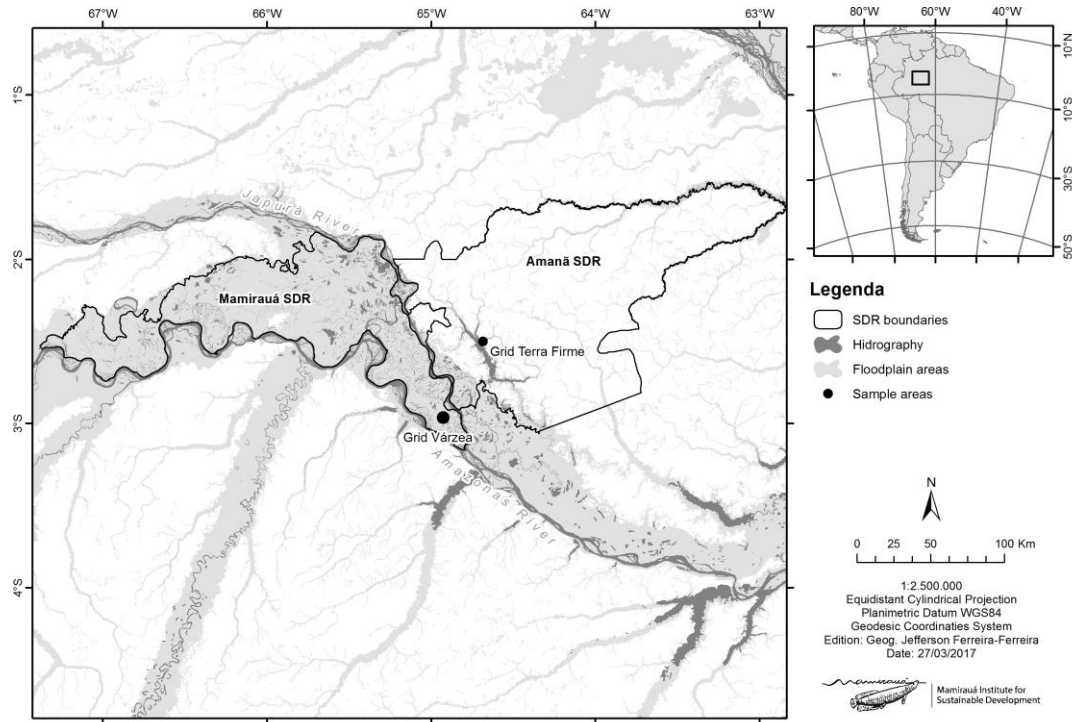


Figure 1. Map of the study areas in Mamirauá Sustainable Development Reserve (MSDR) and Amanã SDR, Central Amazonia, Brazil.

Camera trapping

Sampling was carried out during the low water period of 2013 and 2014.

Fieldwork in MSDR, for both years, occurred between September and December (80 days) in the southeast region of the reserve. For each sampling, 51 camera trap stations were deployed, distributed over an area of 216.5 km², and totaling a sampling effort of 2040 traps*days. For logistic reasons, sampling was divided into two consecutive and continuous blocks, each one installed for 40 days. The first block had 26 camera trap stations and the second 25 stations. The distance between the stations varied from 1.1 to 5.5 km (2.3 ± 0.26 km, mean \pm SD). Each station consisted of two camera traps (model PC800 HyperFire, Reconyx Inc, Holmen, Wisconsin, USA) installed 25 cm from the ground and arranged to face each other, with a 4 m separation.

The camera traps were configured to record species 24 h/day, with no detection interval and a 10-shot frequency (one per second) per detection. Detections of one

species at the same camera trap station in intervals of at least 30 minutes were considered independent. At each station a sardine and egg bait (~ 200 ml) was placed between the two camera traps inside a vented container and fixed to the ground. Baits were renewed at 14 days intervals. In the second year of sampling, 13 camera trap stations on the second block were not baited for approximately 30 days. To evaluate possible mammalian sampling bias due to bait attraction, we compared the total number of species, the total number of records and the number of records of each species between the non-baited (13) and baited camera trap stations (11) using a Student t-test (Online Resource 1). There was no difference between treatments and therefore records from all stations were pooled in analyzes.

Sampling at Amanã, in 2013 and 2014, occurred between December and April (83 days). We used 50 baited camera trap stations, distributed within an area of 130.8 km², giving a total sample effort of 2075 traps*day. Sampling followed the same pattern as in Mamirauá, with two continuous blocks of 25 camera trap stations each separated by 0.9 to 2.0 km (1.6 ± 0.22 km, mean \pm SD). The set up of each camera trap station was the same of described for Mamirauá.

Measuring the várzea forest landscape

Vegetation mapping was performed by Ferreira-Ferreira et al. (2015) in the várzeas of MSDR through Synthetic Aperture Radar (SAR) remote sensing using L-band SAR images (23.6 cm wavelength, 12.5 m spatial resolution) from the PALSAR sensor on board the ALOS satellite, operated by the Japan Aerospace Exploration Agency (JAXA). Besides PALSAR images, were used 5 m spatial resolution RapidEye images (multiple dates between 2009 and 2011) and 2.5 m spatial resolution SPOT-5 (multiple dates in 2014) images were used to support visual interpretation of the landscape (Ferreira-Ferreira et al. 2015).

As a result of the vegetation mapping, the area was divided into five classes: (1) Permanent Water, (2) Soil/Herbaceous Vegetation, (3) Chavascal, (4) Low Várzea and (5) High Várzea. The class Permanent Water represents permanently free water surfaces such as rivers, channels and lakes present even in the driest periods. Soil/Herbaceous Vegetation refers to transient environments dominated mostly by undergrowth and exposed substrate present on the margins of water bodies during periods when the water is low. The last three classes (Chavascal, Low Várzea and High Várzea) are forest formations typical of the white-water floodplain. Chavascal is associated with low-lying, prolonged water-logged soils, and has a low canopy that is dominated by lianas, treelets and shrubs, tolerating floods of 180-240 days per year (water heights varying between 5 and 7 m). Low Várzea comprises arboreal species adapted to flood durations of 120-180 days/year and water level ranging from 2.5 to 5 m. High Várzea tolerates flood durations between 60 and 120 (water level ranging from 1 to 2.5 m) days/year. Their tree assemblage shares around 30% of its species with terra firme forests (Ayres 1993; Wittmann et al. 2010).

To determine the influence of vegetation types on the distribution of mammals in the floodplain, we calculated the occupied area (km²) of each várzea classes at two scales (buffers of 500 and 1000 m radius) around each camera trap station (Online Resource 2). Due to the low knowledge of the mammalian living area of the floodplain forests, we chose the two buffer sizes to capture the possible effect of scale on species with different sizes (Thornton et al. 2010; Jackson and Fahrig 2012; McGarigal et al. 2016). To find the best response scale, both buffers were tested against all response variables. All Geographic Information System (GIS) procedures were conducted using version 2.12.3 of the QGIS program (QGIS, 2016).

Analyses

All statistical analyzes were performed in R, version 3.3.0 (R Core Team, 2011). Due to the regional flood pulse (height and duration of flood) was highly correlated across the two sampling years (Pearson $r^2 = 0.96$), we summed the records of sampling species for both years studying area. We reduced the matrix dimensionality of the medium- and large-sized mammal species recorded in várzea and terra firme using a Non-metric Multidimensional Scaling (NMDS) based on the Bray-Curtis similarity index using the 'vegan' package (Oksanen et al. 2015). We standardized the camera trap stations weight by dividing the number of records of each species by the total number of records of the camera trap station (decostand function, MARGIN = 1). Subsequently, we compared the assemblages of várzea and terra firme using a permutational multivariate analysis of variance (adonis function, 'vegan' package) based on the Bray-Curtis Index with 9999 permutations (Anderson 2005; Oksanen et al. 2015). We compared the total number of records and the number of species in várzea and terra firme mammal assemblages using a Student t-test.

We tested for multicollinearity between the predictor variables (covered areas by Permanent Water, Soil/Herbaceous Vegetation, Chavascal, Low Várzea, High Várzea and Shannon index) using a Pearson correlation. Low Várzea vegetation was correlated with Chavascal (buffer 500 m: $r = -0.64$; buffer 1000 m: $r = -0.71$), and therefore Low Várzea was excluded from the analysis. The Shannon index was calculated using the area (km^2) occupied by each class in the buffers of 500 and 1000 m in each camera trap station (diversity function, 'vegan' package). High values represented greater heterogeneity in the landscape and greater equitability, while low values indicate dominance of an individual class. In order to evaluate the influence of várzea vegetation types on the distribution of medium and large mammals, we used total number of species, total number of records, species composition and number of records of each

mammal species with more than 10 records as response variables (five species). We used a one-axis NMDS solution (Bray-Curtis similarity index) as the mammal species composition. We standardized the species weight on the analysis transforming the number of records of each species in presence or absence. We also tested for spatial autocorrelation of the residuals of the multiple regression response variables using Moran's I index on SAM V.4 software (Rangel et al. 2010). To perform Moran's I index, nine distance classes with equal numbers of connections were used. The upper limits of the distances classes were 1.99, 3.60, 4.82, 5.0, 7.11, 8.3, 9.72, 11.57, 13.57 and 19.06 km. The significance of each Moran's I value was tested with 9999 randomizations. Moran's I values for the nine distance classes were all between -0.19 and +0.12 for all response variables (five species, total number of records, number of species and species composition), indicating that there was no spatial correlation in the mammal occurrence data.

Due to a decrease of calculated spatial metrics independence the overlap between 1 km buffers can lead to, we used Mixed Generalized Linear Models (GLMM) from the 'lme4' R package (Bates et al. 2015). We categorized all buffers so that, those overlapping buffers were grouped in the same category. The categories were then used as a random variable in the GLMMs. We tallied 26 categories, 19 of which had no buffer overlap (only one buffer), four of which had overlap between two-station buffers, one with overlap between three-station buffers, one with overlap between nine-station buffers, and one with overlap between 13-station buffers. Given that the standard error of the random variable intercept was low (<0.3), we decided to use Generalized Linear Models (GLM) in place of GLMM, because former model is simpler and superior at controlling and interpreting data overdispersion. We chose Gaussian distributions (for NMDS values), Poisson (for counting data), Quasipoisson and Negative Binomial (for

overdispersed counting data), according to distribution frequency of the response variable data in a histogram (Zuur et al. 2009). In the analyzes that evaluated the influence of vegetation types on mammal distributions, species with no records from > 50% of camera trap stations were analyzed using Zero Inflation model from the 'pscl' R package (Zeileis et al. 2008; Jackman 2015). The Zero Inflation model separate the data into two sets, (1) values equal to zero and (2) counting values. The excess of zeros are analyze with a GLM Binomial that calculate the probability of find false- and true-zeros. The model then analyze counting values for Poisson distributions (ZIP), once this species counting data are not overdispersed. The assumptions of GLMs and Zeros Inflated model were assayed by plotting the residuals in relation to the adjusted values and quantile-quantile plots (QQ-plot). All the predictors variables of GLMs and Zero Inflated model were scaled using the 'vegan' package (Oksanen et al. 2015). We had two outliers for the species *Coendou prehensilis* and one to *Nasua nasua* that we decided to exclude. However the analyzes with and without those outliers were the same.

Results

Comparisons between várzea and terra firme forests

We obtained 1154 medium and large mammal records in the MSDR várzea and 2289 records in the ASDR terra firme forest. The number of records per effort in terra firme was twice (1.20 record/traps*day) of várzea forest (0.56 record/traps*day) ($t = 5.97$, $P < 0.001$). We recorded 21 species, six in várzea and 20 in terra firme ($t = 18.97$, $P < 0.001$) (Online Resource 3). The ordination of camera trap stations along the two axes of the NMDS explained 95% of the variation in species composition (stress = 0.09) indicating that representation was robust. We observed a marked difference between the

composition of medium and large mammal species for várzea and terra firme forests (PERMANOVA, $R^2 = 0.32$, $P < 0.001$), mainly in axis 1 (Fig. 2). The várzea mammal assemblage represented a subgroup of the terra firme (Fig. 3). Among the 21 species recorded, five occurred in both forest types, 15 species were unique to terra firme, and only *C. prehensilis* exclusively occurs in várzea. Among the few species found in the várzea, *P. onca*, *L. wiedii* and *N. nasua* were recorded more frequently in várzea than in terra firme (Fig. 3).

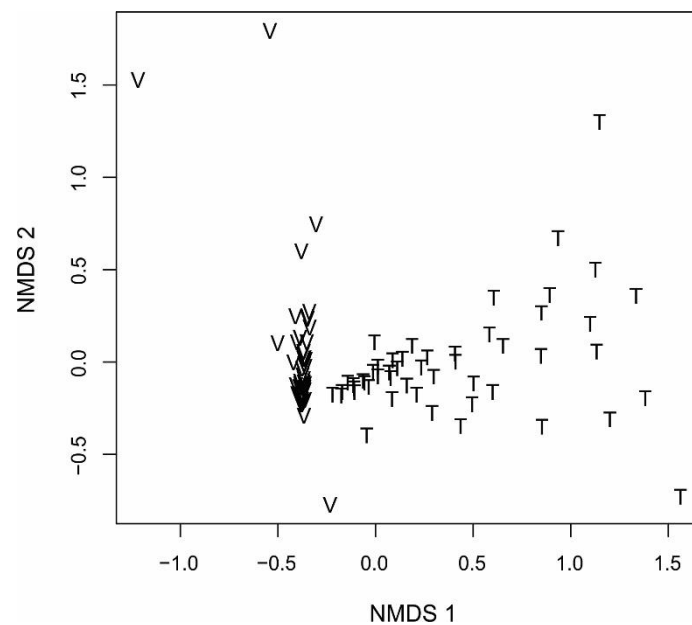


Figure 2. Non-metric Multidimensional Ordination of the medium and large mammal species composition in várzea (V) of Mamirauá Sustainable Development Reserve (MSDR) and terra firme (T) of Amanã SDR, Central Amazonia, Brazil.

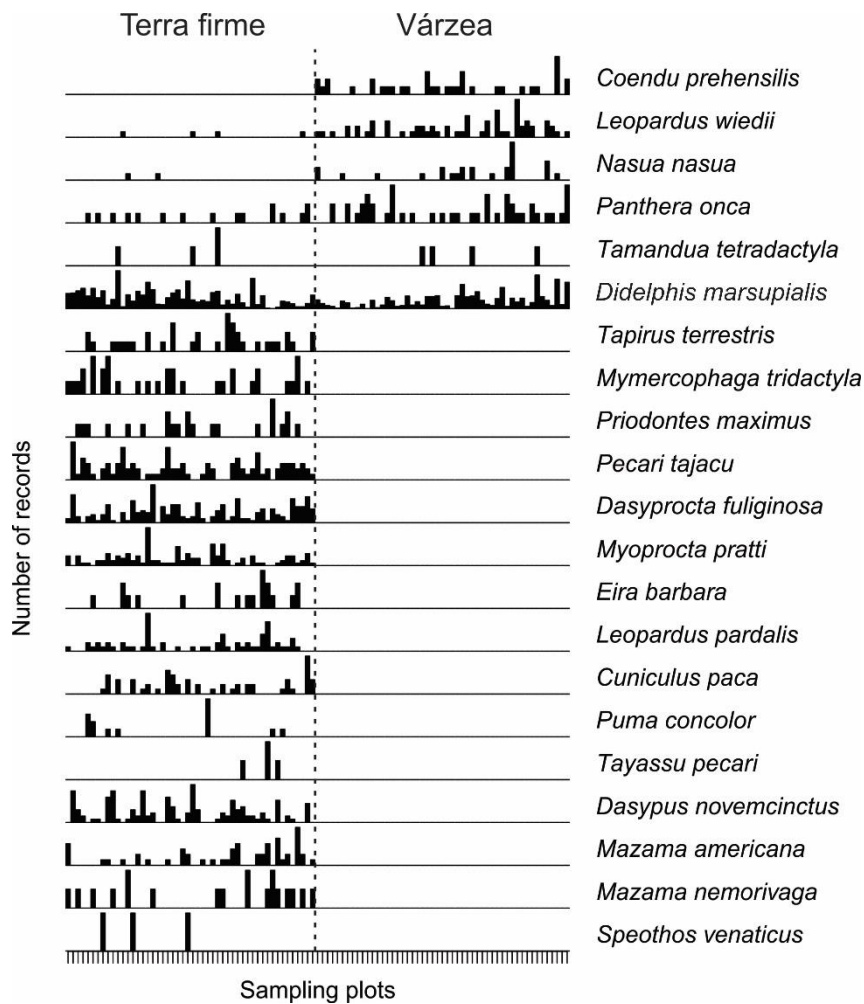


Figure 3. Distribution of the medium and large mammal species records in 101 camera trap stations installed in terra firme forest of Amanã Sustainable Development Reserve and várzea forest of Mamirauá SDR. The dotted line divide the two forest types.

Effect of vegetation types on the distribution of species in várzea forests

As shown by the Shannon index, buffer zone habitat class coverage varied greatly between camera trap stations. Within the 500 m buffer, low várzea was the dominant habitat, occupying an average of $0.44 \pm 0.18 \text{ km}^2$ (mean \pm SD), followed by chavascal ($0.12 \pm 0.16 \text{ km}^2$) and high várzea ($0.13 \pm 0.13 \text{ km}^2$). This pattern was repeated for the 1000 m buffer (Table 1). There were two camera trap stations with dominion low várzea ($H' < 0.05$) in the 500 m buffer. On the other hand, low dominance and high habitat

diversity ($H' > 1.0$) was exhibited for 17 stations in the 500 m buffer and 36 stations in the 1000 m buffer.

Table 1. Area of coverage (km²) of the five habitat classes in várzea of Mamirauá Sustainable Development Reserve, Central Amazonia, and the Shannon index in the 500 m and 1000 m scales buffers around the camera trap stations. Data are presented as mean \pm standard deviation and between parenthesis minimum and maximum values.

| Land cover classes | Scale 500 m | Scale 1000 m |
|--------------------|----------------------------|-------------------------------|
| Water | 0.03 \pm 0.05 (0 - 0.18) | 0.12 \pm 0.13 (0 - 0.59) |
| Soil/Herbaceous | 0.07 \pm 0.08 (0 - 0.39) | 0.25 \pm 0.17 (0 - 0.68) |
| Chavascal | 0.12 \pm 0.16 (0 - 0.56) | 0.55 \pm 0.53 (0 - 1.93) |
| Low Várzea | 0.44 \pm 0.18 (0 - 0.78) | 1.69 \pm 0.57 (0.48 - 2.97) |
| High Várzea | 0.13 \pm 0.13 (0 - 0.48) | 0.51 \pm 0.34 (0 - 1.47) |
| Shannon Index | 0.87 \pm 0.31 (0 - 1.44) | 1.06 \pm 0.25 (0.23 - 1.47) |

In general, with the exception of *P. onca*, mammal species avoided the habitats most susceptible to flooding (Table 2). In the 500 m buffer scale, *C. prehensilis* was the only species with a clear pattern and were positive related to High Várzea forest (Fig. 4a). In the 1000 m buffer, the composition of the mammalian assemblage was influenced by presence of Chavascal (Fig. 4b). The total number of records and *D. marsupialis* were negatively associated with Chavascal (Fig. 4c, d). And, similarly, the number of *N. nasua* records was lower in areas associated with water bodies, Soil/Herbaceous Vegetation and Chavascal (Fig. 4f, g). On the other site, the number of *P. onca* records was lower in High Várzea forest. (Fig. 4h).

Figure 4. Partial regressions of the response variables with significant relation with the habitat classes in várzea forest of Mamirauá Sustainable Development Reserve, Central Amazonia, Brazil.

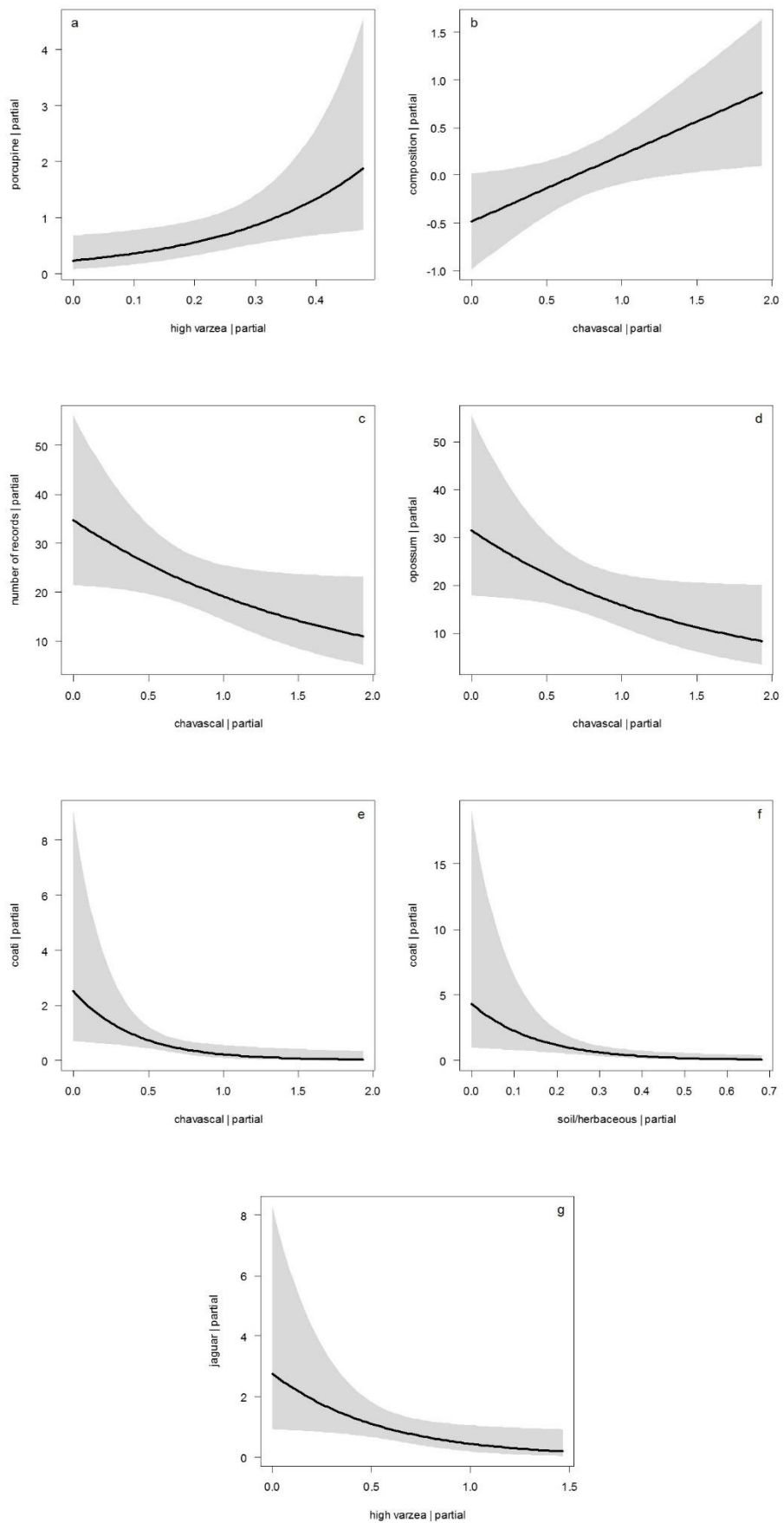


Table 2. Best models result for medium- and large-sized mammals in relation to vegetation types in várzea of Mamirauá Sustainable Development Reserve, Central Amazonia, on the 500 m and 1000 m scales. GLM = Generalized Linear Model; ZIP = Zero-Inflated Poisson. GLM distributions were: G = gaussian; P = poisson; QP = quasi-poisson and NB = negative binomial.

| Scale | Response variable | Permanent Water | | Soil/Herbaceous | | Chavascal | | High Várzea | | Shannon index | | Model |
|--------|------------------------------|-----------------|--------|-----------------|---------|-----------|---------|-------------|---------|---------------|-------|----------|
| | | Estimate | score | Estimate | score | Estimate | score | Estimate | score | Estimate | score | |
| 500 m | Total of records | -0.12 | -0.88 | -0.05 | -0.36 | -0.21 | -1.44 | -0.15 | -1.01 | 0.26 | 1.55 | GLM (NB) |
| | Species composition | 0.11 | 0.77 | 0.18 | 1.15 | 0.28 | 1.83 | 0.07 | 0.41 | -0.26 | -1.41 | GLM (G) |
| | Number of species | -0.02 | -0.17 | -0.06 | -0.51 | -0.14 | -1.19 | -0.06 | -0.51 | 0.11 | 0.89 | GLM (P) |
| | <i>Leopardus wiedii</i> | 0.16 | 0.98 | 0.05 | 0.27 | -0.07 | -0.31 | -0.18 | -0.73 | 0.05 | 0.20 | GLM (QP) |
| | <i>Didelphis marsupialis</i> | -0.16 | -0.98 | -0.06 | -0.38 | -0.22 | -1.27 | -0.15 | -0.87 | 0.29 | 1.46 | GLM (NB) |
| | <i>Panthera onca</i> | -0.45 | -1.69 | 0.04 | 0.21 | -0.22 | -0.86 | -0.56 | -1.94 | 0.25 | 0.90 | GLM (QP) |
| | <i>Coendou prehensilis</i> | 1.68 | 2.04 * | 0.75 | 1.60 | -0.03 | -0.04 | 1.33 | 2.26 * | -0.50 | -0.57 | ZAP |
| | <i>Nasua nasua</i> | -0.11 | -0.29 | -0.79 | -1.59 | -0.78 | -1.76 | -0.60 | -1.36 | 0.34 | 0.80 | ZIP |
| 1000 m | Total of records | -0.20 | -1.28 | -0.14 | -0.99 | -0.32 | -2.01 * | -0.12 | -0.76 | 0.33 | 1.71 | GLM (NB) |
| | Species composition | 0.13 | 0.82 | 0.20 | 1.34 | 0.36 | 2.15 * | -0.38 | -0.02 | -0.19 | -0.96 | GLM (G) |
| | Number of species | -0.05 | -0.40 | -0.08 | -0.66 | -0.14 | -1.05 | -0.01 | -0.08 | 0.07 | 0.48 | GLM (P) |
| | <i>Leopardus wiedii</i> | 0.13 | 0.57 | -0.01 | -0.04 | -0.01 | -0.05 | -0.20 | -0.74 | -0.01 | -0.04 | GLM (QP) |
| | <i>Didelphis marsupialis</i> | -0.25 | -1.34 | -0.17 | -0.99 | -0.37 | -1.96 * | -0.13 | -0.69 | 0.38 | 1.69 | GLM (NB) |
| | <i>Panthera onca</i> | -0.40 | -1.50 | -0.12 | -0.45 | -0.25 | -0.85 | -0.64 | -2.12 * | 0.48 | 1.43 | GLM (QP) |
| | <i>Coendou prehensilis</i> | 0.02 | 0.06 | -0.13 | -0.47 | -0.09 | -0.31 | 0.22 | 0.87 | 0.31 | 0.88 | ZIP |
| | <i>Nasua nasua</i> | -0.66 | -1.24 | -1.86 | -2.40 * | -1.21 | -2.03 * | -0.50 | -1.19 | 0.74 | 1.32 | ZIP |

*P < 0.05, **P < 0.01, ***P < 0.0001

Discussion

Our results show that mammalian assemblages in terra firme and várzea are different at local scale, and that mammalian composition of varzea forests are a subset of the terra-firme forests. Both results, suggest a limited effect of overall species migration between habitats during dry-season. Sampling in Mamirauá várzea was undertaken in the lower Japurá river, where its course is approximately 2 km wide and flows into Amazonas river. For this reason the Mamirauá várzea remains isolated during the dry season, and even species that are strong swimmers, like the jaguar (*P. onca*), avoid crossing the river, in either várzea-terra firme, or terra firme-várzea direction (E. E. Ramalho personal communication). All the species recorded in várzea were semi-arboreal and able to survive in the forest canopy during flooded months.

Number of species

Previous studies at Amanã and Mamirauá reported six species not found in our sampling. However, previous studies used other sampling methods, such as interviews with local residents, direct sighting and shooting. Of the six species, four (*Hydrochaeris hydrochaeris*, *Lontra longicaudis*, *Potos flavus*, *Pteronura brasiliensis*) were recorded in both terra firme and várzea, while two others (*P. concolor* and *T. pecari*) were recorded only in várzea (Bodmer and Ayres 1991; Valsecchi do Amaral 2005). The first four species are semi-aquatic or arboreal, and are difficult to record with camera traps restricted to the understory (Ford and Hoffmann 1988; Emmons and Feer 1997). On the other hand, previous studies at Mamirauá found *P. concolor* and *T. pecari* to be occasional and restricted to the borders of the SDR, suggesting that records may not be from resident populations. It is common to record more species when complementary sampling methods are used, which underscores the importance of using a variety of

techniques when conducting fauna surveys (Silveira et al. 2003; Tobler et al. 2008; Munari et al. 2011). However, the total number of species and the composition of medium and large terrestrial mammal assemblages recorded at Amanã and Mamirauá SDR's were similar to those described in other camera trap-based studies in the Amazon forest (Martins et al. 2007; Tobler et al. 2008; Pickles et al. 2011; Borges 2014; Michalski et al. 2015).

Of the 21 species recorded, four (*Myrmecophaga tridactyla*, *Priodontes maximus*, *Tapirus terrestris* and *Tayassu pecari*) appear as 'vulnerable' on the global IUCN Red List (IUCN 2016). Seven of the recorded species are considered 'vulnerable' at the national level: *Leopardus pardalis*, *L. wiedii*, *M. tridactyla*, *P. onca*, *P. maximus*, *Puma concolor* and *Speothos venaticus* (Chiarello et al. 2008). The presence of these species demonstrates the effectiveness of wildlife conservation in large Protected areas (hereafter 'PAs') in Amazônia (Bruner et al. 2001; Peres 2005). Even predators, such as *P. onca* in Mamirauá SDR and *L. pardalis* in Amanã SDR, that are hunted in retaliation because of attacks on domestic animal, still have stable populations in the reserves (Ramalho 2012; Rocha et al. 2016). However, the continued human population growth in sustainable use PAs constitutes a potential threat to game animals (Peres 2011). In addition, a significant portion of PAs in the Amazonian biome's (~ 42%) are threatened by modifications to existing legislation that will result in changes such as size reduction, diminishing restrictions on human activities, and the full loss of PA status (Bernard et al. 2014). Such threats reinforce the urgent need to document wildlife in PAs and assess their relation to different habitat types, especially for endangered species, to assist management plan formulation (Bernard et al. 2014).

Spatial patterning in mammalian assemblages

Our results show that mammals from várzea are a subset of the species found in terra firme, confirming both our initial hypothesis and the pattern described in the literature for a number of other taxa (Gascon 1996; Ferreira 2000; Haugaasen and Peres 2005; Beja et al. 2010; Bobrowiec et al. 2014). The várzea forest assemblage was composed by semi-arboreal mammals. The same species distribution pattern was described previously using other sampling techniques (Bodmer and Ayres 1991; SCM 1995; Valsecchi do Amaral 2005).

The most plausible explanations for the differences in várzea and terra firme mammalian assemblage composition are linked to seasonal flooding and the isolation of the Mamirauá floodplain by two large rivers, Amazonas and Japurá. The seasonality of the várzea flooding explains the spatial differences for several taxa within the assemblies, especially during the flooding season when the two environments have the greatest contrast (Haugaassen and Peres 2007; Bobrowiec et al. 2014). However, our sampling occurred during the unflooded season, suggesting that other floodpulse-associated factors may contribute to the differences between environments. The Amazonas and Japurá rivers probably act as a barrier to fauna, separating the Mamirauá floodplain from the adjacent mainland forests, producing a pattern similar to that found for primates (Ayres and Clutton-Brock 1992) and terrestrial mammals (Haugaassen and Peres 2005) in other regions of the Amazon basin. Even though taxa such as carnivores, perissodactyls and artiodactyls are known to be strong swimmers, it has been reported that relatively narrow rivers (~ 50 m) can act as barriers to terrestrial mammals in the lower Purus river (Haugaassen and Peres 2005). Therefore, it is not unreasonable to propose that mammal species avoid crossing the Japurá and Amazonas rivers (both slightly > 2 km wide) during the dry season months.

The greater number of records of the terrestrial species in terra firme also indicates the presence of a larger number of individuals and, consequently, may lead a higher total biomass, a pattern that also has been reported in the lower Purus river (Haugaassen and Peres, 2005). The lack of a flood pulse in terra firme makes it possible for terrestrial mammals to live there throughout the year. Strictly terrestrial species such as *T. terrestris*, *P. tajacu*, *T. pecari*, *M. americana* and *M. nemorivaga*, recorded only in terra firme, have a larger body size compared to semi-arboreal species of the floodplain, thus it is possible that have an increasing in the total biomass of mammals in the terra firme forest.

Effects of vegetation on the distribution of mammal species in várzea forest

All response variables were scale-dependent, showing relationships with only one buffer-size. Our results match previous studies in finding a scale-related effect in species response (Gorresen et al. 2005; Thornton et al. 2011; Garmendia et al. 2013; Quesnelle et al. 2014; Muylaert et al. 2016). This pattern is attributed to variations in the coverage of the landscape elements associated with the size of the buffer, as well as species intrinsic factors, such as home range size, ability to move through different landscape types, environmental requirements and life histories (Sutherland et al. 2000; Bowman et al. 2002; Garmendia et al. 2013). Therefore, spatial scale should be taken into account in ecological landscape studies (Jackson and Fahrig 2012; McGarigal et al. 2016; Miguet et al. 2016).

The total number of records and assemblage species composition were influenced by the presence and extent of Chavascal vegetation. The lower number of records in Chavascal supports our hypothesis that environments with extended inundation are avoided by várzea-living mammal species. Factors such as a protracted

inundation period (~ 8 months), and permanently water-logged soils (Wittmann et al. 2004) seems to act as an ecological filter even for semi-arboreal mammal species.

The influence of Chavascal was also evident at the species level, as both *D. marsupialis* and *N. nasua* avoided this habitat. *Nasua nasua* is a gregarious procyonid, with a diet composed mainly of invertebrates and fruits (Gompper and Decker 1998; Alves-Costa et al. 2004), while *D. marsupialis* is a highly adaptable solitary generalist (Charles-Dominique et al. 1981; Estrada et al. 1994). Both species have scansorial habits, but often use the forest floor to move between the trees and for foraging (Miles et al. 1981; Beisiegel and Mantovani 2006; Haugaasen and Peres 2008; Vieira and Camargo 2012), and therefore, tend to avoid the permanently waterlogged Chavascal soils. *Nasua nasua* was also negatively associated with exposed soils and open herbaceous vegetation areas. This exclusively várzea habitat is associated with steep banks (known local as "barrancos") and smooth water bodies' margins (Junk et al. 2011), indicating that *N. nasua* is more sensitive to open areas than other semi-arboreal mammals inhabiting the floodplain. Such avoidance may occur because, open environments with no trees that can be used as escape routes, probably are less safe from predators.

Coudou prehensilis is arboreal; a study in captivity found that it spends 85% of the time in trees (Roberts et al. 1987; Roze 2012). However, the camera traps were set at ground level, so the results for this species should be interpreted with caution. Even so, the distribution of *C. prehensilis* in High Várzea seems plausible. The High Várzea forest has the greatest density and highest number of arboreal species of all floodplain habitats (Ayres 1993; Junk et al. 2011), which helps to explain why most *C. prehensilis* records came from this vegetation type.

The negative association between *P. onca* and High Várzea in Mamirauá could be associated with the distribution of the main prey species (Ramalho and Magnusson 2009). During the non-flooded season, potential prey such as sloths (Queiroz 1995), caiman and their nests are concentrated in low-lying areas transitional between water and land (Silveira et al. 2010), and distant from the High Várzeas (Ayres 1993). In the Viruá National Park, a tendency for the use of flooded environments by individuals of *P. onca* was also observed (Palomares et al. 2017). Generally, large felines tend to alter their use of space depending on prey availability (Sunquist and Sunquist 1989; Crawshaw and Quigley 1991; Mendes Pontes and Chivers 2007). Spatial utilization by *L. wiedii* could also be associated with prey distribution. However, 21 known *L. wiedii* prey species were recorded, ranging from arboreal mammals, birds, lizards and amphibians (Oliveira 1998). This variety of available prey probably allows *L. wiedii* to use the various várzea habitats in a more homogeneous way and therefore no precise habitat association was been found for this species in várzea.

Conservation implications

Our results indicate that várzea vegetation types influence the distribution of medium- and large-sized mammals. Our understanding about the use dynamics of the different várzea environments by terrestrial mammals needs further focused studies for effective management planning. However, the low number of species found in várzea does not imply that this environment should be neglected during conservation planning. On the contrary, a variety of studies have shown that many species use seasonally the flooded forests in more connected environments, suggesting that a combination of flooded and non-flooded environments is crucial to the long term maintainance of viable populations (Janson and Emmons 1990; Bodmer 1990; Emmons and Feer 1997; Peres 1999; Hugaasen and Peres 2007). The importance of preserving large areas of adjacent

várzea and terra firme forests is shown by the high species turnover between these environments. Some felines species (*P. concolor* and *L. pardalis*) and large mammals (deer, peccaries and tapir) were recorded exclusively in terra firme forests, while other felines (*P. onca* and *L. wiedii*) were more common in várzea. Várzea forests have been identified as an important environment for preservation of a diverse range of animal groups, including fish (Castello 2008), amphibians (Gascon 1996), primates (Barnett et al. 2013; Rabelo et al. 2014) and bats (Bobrowiec et al. 2014). However, floodplains are been constantly and consistently threatened by such human activities as hunting, and the creation of areas for grazing cattle and raising crops (Junk and Piedade 2010). The low resilience of lowland forests makes them extremely susceptible to collapse, which would impact the entire Amazon basin (Flores et al. 2017).

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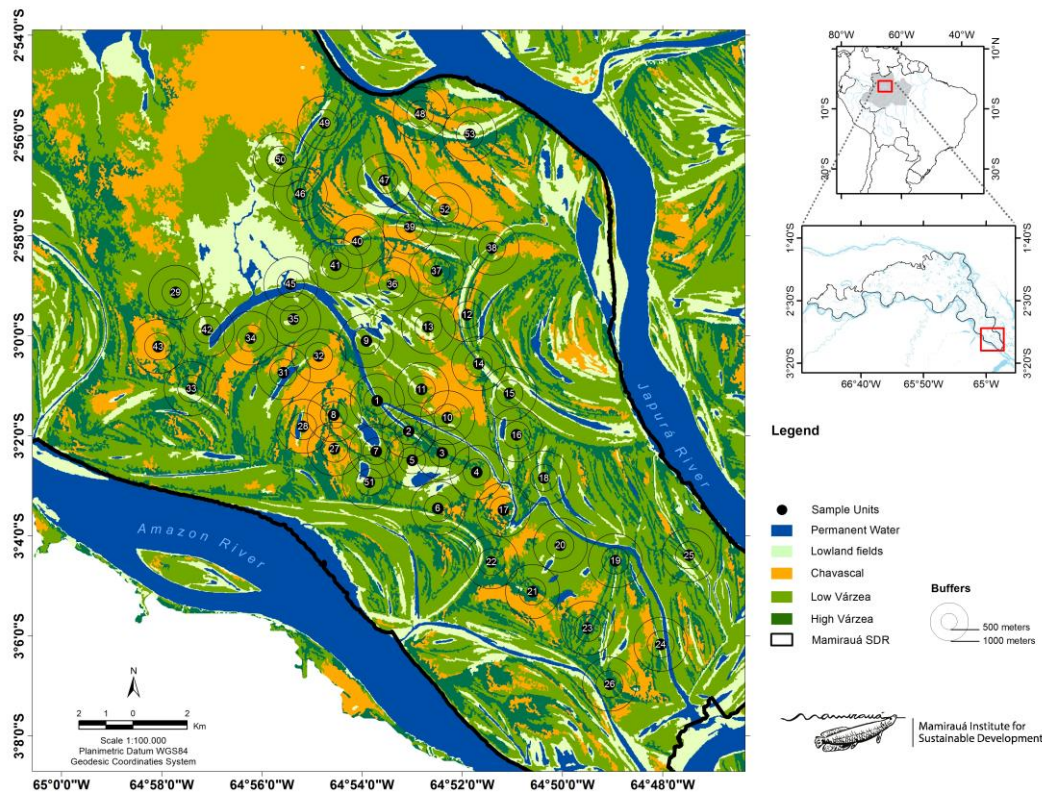
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Supplements

Online resource 1. Student *t*-test to evaluate the possible influence of the use of bait in the record of medium and large mammal species in camera trap stations in várzea of Mamirauá Sustainable Development Reserve, Central Amazonia, Brazil. ‘No bait’ is a comparison of baited and unbaited stations, while ‘Control’ is a comparison of station with the same treatment.

| Response variable | No bait | | Control | |
|------------------------------|----------|------|----------|------|
| | <i>t</i> | p | <i>t</i> | p |
| Total of records | 1.46 | 0.16 | -0.85 | 0.41 |
| Number of species | 1.63 | 0.12 | -2.10 | 0.06 |
| <i>Leopardus wiedii</i> | -2.15 | 0.08 | 1.73 | 0.22 |
| <i>Didelphis marsupialis</i> | 1.61 | 0.13 | -0.95 | 0.36 |
| <i>Panthera onca</i> | 3.00 | 0.20 | -0.50 | 0.66 |
| <i>Coendou prehensilis</i> | - | - | 0.41 | 0.69 |
| <i>Nasua nasua</i> | - | - | -4.00 | 0.06 |

Online resource 2. Distribution of 51 camera trap stations and respectively buffers in both scales, 500 m and 1000 m, in the Mamirauá Sustainable Development Reserve. Each color represent a habitat class of várzea forest.



Online resource 3. Medium and large mammal species records and the number of camera trap stations with records in várzea and terra firme forests, Central Amazonia, Brazil.

| Species | Várzea | | Terra firme | |
|--------------------------------|---------|----------|-------------|----------|
| | Records | Stations | Records | Stations |
| <i>Didelphis marsupialis</i> | 977 | 48 | 1296 | 49 |
| <i>Leopardus wiedii</i> | 64 | 31 | 4 | 4 |
| <i>Panthera onca</i> | 46 | 28 | 16 | 14 |
| <i>Nasua nasua</i> | 26 | 14 | 2 | 2 |
| <i>Tamandua tetradactyla</i> | 4 | 4 | 4 | 3 |
| <i>Coendou prehensilis</i> | 37 | 25 | 0 | 0 |
| <i>Tapirus terrestris</i> | 0 | 0 | 37 | 24 |
| <i>Myrmecophaga tridactyla</i> | 0 | 0 | 35 | 23 |
| <i>Priodontes maximus</i> | 0 | 0 | 23 | 18 |
| <i>Pecari tajacu</i> | 0 | 0 | 102 | 41 |
| <i>Dasyprocta fuliginosa</i> | 0 | 0 | 258 | 46 |
| <i>Myoprocta pratti</i> | 0 | 0 | 138 | 42 |
| <i>Eira barbara</i> | 0 | 0 | 20 | 14 |
| <i>Leopardus pardalis</i> | 0 | 0 | 65 | 34 |
| <i>Cuniculus paca</i> | 0 | 0 | 57 | 23 |
| <i>Puma concolor</i> | 0 | 0 | 14 | 7 |
| <i>Tayassu pecari</i> | 0 | 0 | 4 | 3 |
| <i>Dasypus novemcinctus</i> | 0 | 0 | 139 | 35 |
| <i>Mazama americana</i> | 0 | 0 | 53 | 24 |
| <i>Mazama nemorivaga</i> | 0 | 0 | 19 | 16 |
| <i>Speothos venaticus</i> | 0 | 0 | 3 | 3 |
| Total | 1154 | 51 | 2292 | 50 |

Conclusão Geral

Em uma realidade na qual a floresta Amazônica vem perdendo área com o avanço das pressões antrópicas, a partir da construção de estradas, aumento da área urbana e substituição de floresta para atividades agrossilvopastoris. O desenvolvimento de pesquisas que nos auxiliem a entender como a fauna se distribui no ambiente se tornam essenciais. Os mamíferos representam uma parcela significativa da biomassa animal das florestas e, além disso, são responsáveis por diversas funções ecológicas, como pisoteamento de plântulas e dispersão de sementes. No entanto, muitas regiões da Amazônia continuam mal amostradas, de modo que decisões conservacionistas se tornam ineficazes. Nosso trabalho contribuiu para aumentar o conhecimento sobre a distribuição dos mamíferos em ambientes de várzea, sendo o primeiro trabalho a analisar como os mamíferos de médio e grande portes respondem à variação das fitofisionomias da várzea. Sugerimos que mais trabalhos sejam desenvolvidos em outras regiões da várzea Amazônica, já que as características peculiares da várzea de Mamirauá podem interferir na resposta das espécies que lá habitam.