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Movimentos sazonais de vertebrados terrestres entre florestas periodicamente alagadas e de terra firme

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SUMÁRIO

Seasonal movements of terrestrial vertebrate between Amazonian flooded and unflooded forests

ABSTRACT

The flood pulse is the main factor structuring and differentiating the ecological communities of Amazonian unflooded (*terra firme*) and seasonally-flooded (*várzea*) forests as they require unique adaptations to survive the prolonged annual floods. Therefore, *várzea* and *terra firme* forests hammer out a spatio-temporal mosaic of resource availability, which may result in landscape scale seasonal movements of terrestrial vertebrates between adjacent forest types. Yet the lateral movements of terrestrial vertebrates between hydrologically distinct neighbouring forest types exhibiting staggered resource availability remains poorly understood, despite the important implications of this spatial dynamic for the ecology and conservation of forest wildlife. We examined the hypothesis of seasonal movements between two adjacent forest types at two contiguous sustainable-use forest reserves in Western Brazilian Amazonia, investigating the effects of water level, landscape and anthropogenic disturbance on the overall species richness, composition, and abundance of nine major vertebrate trophic guilds. Species richness differed in neighboring *terra firme* forests between the high-and low-water phases of the flood pulse and *terra firme* forests were more species rich than *várzea* forests. There were clear differences in species composition between both forest types and seasons. Generalized Linear Models showed that water level was the main factor explaining aggregate abundance of all species and three trophic guilds. Anthropogenic disturbance and geographic setting of camera trap stations, including distance to the nearest urban center, the number of residents of the nearest community, elevation and the surrounding area of *várzea* of each camera trap station, had a variety of effects on the terrestrial vertebrate assemblage. Overall vertebrate biomass increased with distance from the nearest urban center. Our results indicate that the persistence of viable populations of large terrestrial vertebrates adjacent to major Amazonian rivers requires large, wellconnected forest landscapes encompassing different forest types to ensure large-scale lateral movements by forest wildlife.

Keywords: camera-trapping, flood pulse, floodplain dynamics, *várzea*, wetlands

Movimentos sazonais de vertebrados terrestres entre florestas periodicamente alagadas e de terra firme

RESUMO

O pulso de inundação é o principal fator para a estruturação e diferenciação das comunidades ecológicas de florestas de terra firme e de várzea na Amazônia, uma vez que são requeridas adaptações exclusivas para sobreviver às prolongadas enchentes anuais. Desta forma, as várzeas e a terra firme constituem um mosaico espaço-temporal da disponibilidade de recursos, o qual provavelmente resulta em um movimento lateral e sazonal na fauna terrestre entre esses dois ambientes adjacentes. Apesar das importantes implicações desta dinâmica sazonal para a ecologia e conservação da biodiversidade este fenômeno ainda é pouco conhecido. Nós testamos a hipótese de movimentação sazonal entre dois tipos florestais adjacente em duas reservas de uso sustentável na Amazônia ocidental, investigando os efeitos do nível da água bem como características da paisagem e de distúrbio antropogênico sobre a riqueza, composição e abundancia de nove guildas tróficas de vertebrados terrestres. A riqueza de espécies se diferenciou entre as fases seca e cheia do pulso de inundação, florestas de terra firme apresentaram maior riqueza do que as florestas de várzea. Encontramos uma clara diferença na composição de espécies tanto entre as duas fases do pulso de inundação quanto entre os dois tipos florestais. Os modelos lineares generalizados mostram que o nível da água é a principal variável para explicar a variação na abundancia de todas espécies e de três guildas tróficas em particular. As caraterísticas da paisagem e variáveis de distúrbio antopogenico, incluindo distância para o centro urbano mais próximo, elevação e área de várzea no entorno de cada armadilha fotográfica apresentaram uma variedade de efeitos sobre a assembleia de vertebrados terrestres. A biomassa total apresentou uma relação positiva com a distância do centro urbano mais próximo. Nossos resultados indicam que a persistência de populações viáveis de grandes vertebrados terrestres em regiões adjacentes aos grandes rios Amazônicos, requer grandes paisagens bem conectadas e que englobem diferentes formações florestais para assegurar os movimentos laterais d fauna terrestre.

Palavras-chave: armadilhas-fotográficas, pulso de inundação, várzea, áreas úmidas

INTRODUÇÃO GERAL

O uso do hábitat pode ser definido como a maneira em que um indivíduo ou uma espécie utiliza os recursos físicos e biológicos do ambiente para sua alimentação, reprodução, fuga de predadores e/ou de competidores. As várias atividades de um animal requerem condições ambientais específicas que podem variar sazonalmente de forma que diferentes espécies podem exercer alguma forma de partição de habitat em diferentes escalas temporais (Krausman 1999). A seleção do hábitat por uma espécie pode ser entendida como um processo hierárquico de decisões inatas e comportamentais sobre qual tipo de hábitat será usado em diferentes escalas ambientais (Hutto 1985).

Diferentes fatores influenciam a seleção do habitat por uma espécie ou indivíduo. A competição, intraespecífica ou interespecífica, pode determinar qual tipo de hábitat será selecionado ou mesmo restringir a distribuição espacial devido à partição dos recursos disponíveis (Palomares et al. 1996, Sollmann et al. 2012). A existência de predadores pode restringir a ocupação de uma área pelas espécies, sendo a reprodução e sobrevivência as forças ecológicas que direcionam a seleção do hábitat a ser utilizado (Block & Brennan 1993). Uma vez que os predadores são removidos, áreas com recursos disponíveis podem ser novamente ocupadas.

De acordo com Dunning et al. (1992), a complementaridade e suplementação dos habitats são fatores importantes na dinâmica das populações e na estruturação das comunidades de ambientes complexos como as florestas tropicais. Em habitats complementares, as espécies se movimentam pelos diferentes ambientes para obter recursos não-substituíveis, ou seja, os habitats possuem uma série de recursos exclusivos ou que são raros em outros habitats, determinando a utilização obrigatória de um mosaico de vários tipos ambientes, enquanto que em habitats suplementares, o recurso não é exclusivo de algum tipo de habitat, mas a utilização de diferentes ambientes ainda se faz necessária para que a quantidade mínima de determinado recurso seja obtida, portanto, independente do tipo de recurso a ser obtido (não-substituível ou substituível), em uma paisagem complexa as espécies necessitam transitar por diferentes habitats.

A Amazônia, com cerca de sete milhões de quilômetros quadrados, é a maior e mais biodiversa floresta tropical do mundo, abrigando cerca de um terço de toda a diversidade global (Azevedo-Ramos et al. 2006). A vegetação Amazônica é formada por um mosaico de habitats distintos que incluem florestas de transição, matas secas, matas semidecíduas, matas de bambu, campinaranas, enclaves de cerrado, buritizais, florestas alagáveis (igapós e várzeas), e principalmente por florestas de terra firme, os quais podem ocorrer em uma mesma localidade.

Florestas de terra firme constituem a maior parte do território Amazônico, são formadas em solos bem drenados que tendem a ser fortemente lixiviados e pobres em nutrientes por serem privados de sedimentos aluviais. Porém, vários tipos florestais podem ser encontrados nestes ambientes devido à uma combinação de fatores edáficos, topográficos e ecológicos (Tuomisto et al. 1995). As florestas e os campos alagáveis compreendem aproximadamente 30% da bacia Amazônica sendo que cerca de 250 mil quilômetros quadrados são ocupados por florestas periodicamente inundadas por rios de água branca como o Amazonas (Solimões), Japurá, Madeira e Juruá e são localmente conhecidas como várzeas (Prance 1979, Junk et al. 2011). As inundações periódicas dos rios de água branca transformam a paisagem criando um gradiente de sucesão de vegetação favorecendo a heterogeneidade ambiental e regeneram os solos com ricos sedimentos drenados da Cordilheira dos Andes constituindo ambientes de grande produtividade primária (Wittmann et al. 2006, Junk et al. 2011).

Em conjunto, esses processos podem explicar a grande diversidade de mamíferos da Amazônia Ocidental (Voss & Emmons 1996, Peres 1997a, Haugaasen & Peres 2005b, Salvador et al. 2011) não somente pela diversidade ambiental mas também pela assíncrona produção de frutos entre as diferentes formações florestais originando um mosaico espaço-temporal de recursos para a mastofauna local (Haugaasen & Peres 2007). A produção de frutos das florestas de terra firme e das florestas alagáveis ocorre de forma complementar, enquanto o ápice da frutificação das florestas de terra firme se dá no início da estação chuvosa, nos ambientes de várzea e igapó os frutos iniciam sua maturação quando os rios já estão cheios (Schöngart et al. 2002, Haugaasen & Peres 2005a, 2007). Alguns estudos têm descrito comparativamente a composição e a estrutura da comunidade de mamíferos terrestres de médio e grande porte de florestas de terra firme e de florestas alagáveis (Bodmer 1990; Haugaasen & Peres 2005b, Tobler et al. 2008, Salvador et al. 2011). As florestas de terra firme são mais ricas em espécies e apresentam um maior número de especialistas do que as florestas alagáveis, enquanto que a biomassa e a densidade de folívoros é maior nas florestas periodicamente inundadas (Peres 1997b, 1999; Haugaasen & Peres 2005b). Apesar de se apresentarem estruturalmente diferentes, é de se esperar que o uso sazonal desses tipos florestais seja vital para a mastofauna regional uma vez que a diversidade de habitats em ambientes de terra firme tende a ser menor e a baixa disponibilidade de recursos alternativos durante o período de escassez de frutos pode reduzir severamente a capacidade deste tipo florestal abrigar grandes populações de frugívoros e herbívoros que seriam atraídos pela maior disponibilidade de sementes e frutos acumulados no chão da várzea imediatamente após a redução do nível do rio e consequentemente também ocupada por seus predadores (Haugaasen & Peres 2007, Mendes Pontes & Chivers 2007). Este estudo buscou investigar a dinâmica sazonal de vertebrados terrestres em florestas de várzea e de terra firme quantificando a sua abundancia relativa durante as duas fases do pulso de inundação. É predito que a riqueza de espécies, a abundancia e a biomassa de vertebrados terrestres em florestas de terra firme durante a fase cheia será maior do que durante a fase seca. Este contraste na abundancia de espécies indicará que a fauna terrestre deixa a terra firme e se move para a várzea devido à alta quantidade de recursos disponível neste ambiente durante. Desta forma, deverá ocorrer uma alta abundância de vertebrados terrestres na terra firme adjacente à várzea causada pelo movimento lateral da fauna deixando a várzea no início da estação cheia.

Para testar esta hipótese, instalamos armadilhas fotográficas tanto em florestas de várzea quanto em florestas de terra firme ao longo de um grande rio afluente do Solimões durante as duas fases do pulso de inundação. Examinamos diferenças na abundancia, riqueza e mudanças na composição de espécies entre os dois tipos florestas e entre as duas fases do pulso de inundação, bem como a influência de características da paisagem e variáveis de distúrbio antropogênico.

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Capítulo 1

Seasonal dynamics of terrestrial vertebrate abundance between Amazonian flooded and unflooded forests

O capítulo I desta Dissertação foi elaborado e formatado conforme as normas da publicação científica *PEER J*, as quais se encontram em anexo (Anexo I)

Seasonal dynamics of terrestrial vertebrate abundance between Amazonian flooded and unflooded forests

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Introduction

Wetland habitats are both challenging to conserve and globally important for biodiversity conservation and human wellbeing (Keddy et al., 2009). Seasonal and perennial wetlands are globally important and exceptionally productive habitats that support both high densities and a high diversity of wild species (Halls, 1997; Junk et al., 2006). They also directly underpin the livelihoods of millions of people and provide ecosystem services including productive fisheries, water purification, hydrological regulation, nutrient cycling and naturally-fertilized agricultural land (Costanza et al., 1997; François et al., 2005). The associated seasonal movements of wetland fauna are especially challenging to conserve because their spatially complex life histories require resources provided by several distinct habitats and entail diverse anthropogenic threats at multiple sites (Martin et al., 2007; Wilcove & Wikelski, 2008).

Hunted migratory species — including salmonids, bats, passerines, waterfowl and grassland ungulates — often contend with severe demographic depletion due to unsustainable offtake (Madsen & Fox, 1995; Dudgeon et al., 2006; Bolger et al., 2007; McCulloch, Tucker & Baillie, 2008; Epstein et al., 2009). Overharvesting may be exacerbated by a “tragedy of the commons” whereby human harvesters have little incentive to conserve their common-pool resource stock in the absence of communal resource management institutions or governance norms (Ostrom, 2008). Species which form large aggregations during migrations are especially attractive targets to human hunters, who can maximize the return on their foraging investment by slaughtering many individuals in a short period (Peres, 1996).

A vast proportion of the Amazon Basin is formed by natural landscape mosaics of wetlands embedded within a matrix of upland (hereafter, *terra firme*) forests on generally nutrient-poor soils well above the maximum water-level of adjacent floodplains (Tuomisto et al., 1995). Amazonian floodplains comprise a variety of habitats including swamp forests, hydromorphic savannas, coastal wetlands, tidal forests, and seasonally-flooded forests. These Amazonian wetlands are classified according to their climatic, edaphic and floristic characteristics (Junk & Piedade, 2010; Junk et al., 2011). Based on these criteria, two large groups of wetlands have been broadly distinguished: those with either (i) relatively stable or (ii) oscillating water levels (Junk et al., 2011).

Most Amazonian wetlands with oscillating water levels are subjected to a predictable, long-lasting monomodal flood pulse which alternates between the high- and low-water periods according to the Flood Pulse Concept (Prance, 1979; Junk, Bayley & Sparks, 1989). Depending on the geomorphology and geochemical profile of each watershed, these areas can be inundated by white-, black- or clear-water rivers (Sioli, 1984). White-water rivers such as the Solimões, Madeira, Japurá and Juruá have their origins in the Andes or Andean piedmonts, are nutrient-rich, and have neutral pH. These rivers deposit their alluvial sediments along wide swaths of floodplain forests of high primary productivity, which are locally known as *várzeas* (Wittmann et al., 2006; Junk et al., 2011). In contrast, Amazonian black-water rivers such as the Negro, Tefé and Jutaí rivers discharge transparent-blackish waters with low suspended sediment loads and acidic pH. Forests inundated by black-water rivers are locally known as *igapós* and are typically supported by low-fertility soils and their trees exhibit 50% lower diameter increment compared to *várzea* forests (Junk & Piedade, 2010; Junk et al., 2011).

The flood pulse is the main factor structuring and differentiating the ecological communities of *várzea* and *igapó* forests from adjacent *terra firme* forests (Peres, 1997; Haugaasen & Peres, 2005a, Haugaasen & Peres, 2005b; Beja et al., 2009) as they require unique adaptations to survive the prolonged annual floodwaters. *Terra firme* forests are more species-rich, including more forest habitat specialists than *várzeas* and *igapó*, while the average population biomass density is higher in seasonally-flooded forests along white-water rivers (Peres, 1997). This predictable long-lasting and monomodal flood pulse triggers and synchronizes critical ecological events including the availability of plant reproductive parts (Nebel et al. 2001, Schöngart et al. 2002, Haugaasen & Peres 2005a, Hawes & Peres 2016), dietary shifts in primates, ungulates and fishes (Bodmer 1990, Peres 1994, 1999, Saint-Paul et al. 2000), human extractive activities of non-timber forest products, and the exploitation of both terrestrial and aquatic prey (Newton, Endo & Peres 2011; Endo, Peres & Haugaasen 2016).

As they are structurally and compositionally different, Amazonian *várzeas*, *igapós* and *terra firme* forests engender a spatio-temporal mosaic of resource availability which may result in landscape-scale seasonal movements of terrestrial vertebrates between these often neighbouring forest types (Bodmer 1990, Peres 1999, Haugaasen & Peres 2007). *Terra firme*, *várzea* and *igapó* forests exhibit complementary fruit production peaks, whereby the fruiting peak in *terra firme* forests occurs during the onset of the wet season, whereas fruit maturation in *várzeas* and *igapós* begin during the late high-water season (Schöngart et al., 2002; Haugaasen & Peres, 2005a, 2007; Hawes & Peres, 2016).

This asynchrony in fruit production attracts frugivorous fish and arboreal frugivores to floodplain forests during the high-water period (Saint-Paul *et al.* 2000; Beja *et al.* 2009), whereas ungulates, carnivores, terrestrial insectivores and ant-following birds are attracted to *várzeas* and *igapós* immediately after the water level recedes. These lateral movements are due to the high abundance of fruit and seed deposited on the forest floor and higher insect abundance during this period

(Bodmer 1990, Peres 1994, Adis & Junk 2002, Haugaasen & Peres 2007, Mendes Pontes & Chivers 2007, Beja et al. 2009).

Our study seeks to investigate the seasonal dynamics of terrestrial vertebrates in Amazonian seasonally-flooded and unflooded forests by quantifying their relative abundance during both the high- and low-water phases of the flood pulse. We predict that the species richness, abundance and biomass of terrestrial vertebrates in *terra firme* forests adjacent to seasonally-flooded *várzea* forests during the flood pulse will be higher than during the low-water phase. This abundance contrast would indicate that the terrestrial fauna most likely leave *terra firme* forest and move into *várzea* forests during the low-water phase to take advantage of higher resource availability. Conversely, there should be transient overcrowding of the terrestrial vertebrate fauna in adjacent *terra firme* forests driven by lateral movements away from the rising floodwaters during the high-water phase.

To test this hypothesis we conducted camera-trapping surveys in both *terra firme* and *várzea* forests along a major white-water tributary of the Amazon river during the high- and low-water phases of the flood pulse. We examined differences in vertebrate abundance, species richness, and changes in species composition between these two forest types and seasons and the associated effects of geographic or landscape setting of camera traps in relation to anthropogenic disturbance. We provide crucial empirical evidence supporting the notion that Amazonian *terra firme* and *várzea* forests should be juxtaposed within fully functional floodplain protected areas, thereby enhancing both the spatial configuration of reserve design and landscape management of highly heterogeneous forest macromosaics in Amazonia for both biodiversity persistence and the subsistence of local extractive communities.

Materials & Methods

Study Area

This study was carried out in two contiguous sustainable-use forest reserves within the State of Amazonas, Brazil: the Médio Juruá Extractive Reserve (RESEX) spanning 253,227 ha, and the Uacari Sustainable Development Reserve (RDS) spanning 632,949 ha. Both reserves border the white-water Juruá River, the second largest white-water tributary of the Amazonas/Solimões River. These protected areas contain large expanses of *terra firme* forests (80% of both reserves) as well as an approximately 18.40 ± 5.71 km wide band of seasonally-flooded *várzea* forest (17.9%) encompassing the main river channel (Hawes et al., 2012) (Fig. 1). The Juruá region experiences an Af climate type (constantly humid) according to Köeppen criteria, with a mean annual temperature of 27.1ºC, a mean rainfall of 3,679 mm/year, and peak water levels of 8 - 12 m during a prolonged flood pulse, which is alternated by a dry phase in *várzea* between July and early

November (Peres, 1997). The regional elevation range is 65 – 170 m above sea level. All forest sites surveyed consist of largely undisturbed primary forest, although commercially valuable timber species have experienced small-scale selective logging along the Juruá River from 1970 to 1995, especially in *várzea* forests.

The RESEX Médio Juruá and RDS Uacari were created in 1997 and 2005, respectively, and are currently inhabited by some 4,000 legal residents, distributed across 74 local communities. These communities are located on both sides of the Juruá River, adjacent to either the main river channel or tributaries and oxbow lakes. Residents of these reserves are variously engaged in agricultural and extractive activities for both subsistence and cash income (Newton, Endo & Peres, 2011; Campos-Silva & Peres, 2016).

Camera trapping

Data on the relative abundance of terrestrial vertebrates were collected at 279 camera-trapping stations (CTS) deployed at distances of 3,100 ± 367 m ($\bar{x}$ ± SD) apart, along a ~514-km nonlinear section of the Juruá River (Fig. 1). We used Bushnell Trophy Cam 119436c, Reconyx Hyperfire HC500 and Bushnell 8MP Trophy Cam HD camera traps. These were programmed to record three and five consecutive photographs and 10-sec videos, respectively, at each trigger event without intervals. A CTS consisted of one camera trap deployed 40-60 cm above ground, and operated over a functional period of 38.7 ± 13.9 days (≈ 928.8 ± 333.6 hours). The sensor sensitivity was set to high, and all CTS were unbaited and deployed away from trails.

Camera-trapping stations were deployed in two complementary sample designs (Table 1; Fig. 1): From April 2013 to June 2014, 193 CTS were deployed at intervals of 50m, 350m, 1000m, 3000m and 6000m Euclidean distance along transects, arrayed in contiguous *terra firme* primary forest, radiating away from local communities. This design facilitated surveys of terrestrial vertebrate abundance at varying distances from the *várzea* interface and at varying intervals during the receding flood pulse. In the second design, repeated over two inundation (March-April 2013 and 2015) and two low-water phases (September-October 2013 and 2014), CTS were deployed in both *várzea* forests and adjacent *terra firme* sites. In this arrangement, *terra firme* CTS were deployed during both high- and low-water phases whereas *várzea* CTS were surveyed only during the low-water phase, as *várzea* habitat is only available to the terrestrial fauna during this time of year.

Data management and estimates of the number of independent detections were undertaken using *camtrapR* version 0.99.8 (Niedballa et al., 2016). Images of conspecifics >30 min apart were defined as independent detection events. Species nomenclature followed the IUCN Red List (IUCN 2013). Primates, non-terrestrial birds and rodents and marsupials smaller than 1 kg were excluded from our analyses, but all other avian and mammalian taxa were considered. Congener brocket deer (*Mazama* spp.), armadillos (*Dasypus* spp.), and small tinamous (*Crypturellus* spp.) were each treated as single species functional group due to difficulties in differentiating them in nocturnal (black and white) images.

All species considered here were grouped into nine trophic guilds (frugivore-insectivores, granivore-frugivores, frugivores, carnivores, frugivore-carnivores, insectivore-frugivores, insectivores, browsers and frugivore-browsers) based on Benchimol & Peres (2015). An assemblage-wide metric of aggregate biomass was calculated by multiplying the species-specific camera-trap detection rate (number of detections/100 trap-nights) by the mean adult body mass per species, which could then be summed across all species detected at each CTS. For group-living species, we multiplied individual body mass values by the mean observed group size obtained from line-transect surveys conducted in the same study landscape (Abrahams, Peres & Costa, 2017).

For each CTS, we extracted landscape and human disturbance covariates using ArcGIS (version 10.3) (Table 2). We calculated the mean water level of the Juruá River during the exposure period of each CTS using daily water-level readings, recorded over 38 years (from 1st January 1973 to 31st December 2010; $N \approx 14{,}600$ measurements) at a nearby locality (Gavião Metereological Station in Carauari-AM). As a continuous variable, mean water-level during CTS sampling intervals was a far more powerful descriptor of seasonality period than either categorical season (e.g. low-water vs high-water season) or time of the year (e.g. Julian day) per se.

Data analysis

All analyses were conducted in R version 3.3.2 (R Core Development Team 2016). We first used both Student’s paired t-tests and ordinary t-tests to examine differences in species richness and abundance of *terra firme* forests between the high- and low-water phases, and between *terra firme* sites during the low-water phase and *várzea* forests, respectively. We estimated species richness per CTS, accounting for any differences in the number of trap nights, using a rarefaction method and first-order Jackknife estimator available in the *specaccum* function of the “vegan” package of R. We choose this estimator because it gives the most reliable results in tropical forest camera-trap studies (Tobler et al., 2008). For the abundance analyses, we considered the camera-trapping rate (number of independent detections per 100 trap-nights) as our response variable. These analyses were performed using CTS data from our second sample design.

To assess the effects of forest type and season on terrestrial vertebrate assemblage structure, we used Principal Coordinates Analysis (PCoA) using a Bray–Curtis similarity distance matrix. Prior to these analyses, to reduce the weight of abundant species in the ordination space, terrestrial vertebrate abundance was standardized by dividing the number of detections of each species by the total number of detections at each CTS. Differences in species composition between forest types, and seasons were tested using Permutational Multivariate ANOVA (PERMANOVA) (Anderson, 2001) performed using the Bray-Curtis similarity matrix. To test for seasonal effects on species composition at *terra firme* CTS, we performed a Procrustes rotation analysis of the ordination matrices derived from CTS that were surveyed during both the high- and low-water phases of the flood pulse. In the PCoA and PERMANOVA analyses, we employed all CTS, whereas the Procrustes rotation was performed using only the data from the second sample design.

We tested the hypothesis of seasonal faunal movement between forest types and investigated the effects of landscape context and anthropogenic disturbance employing Generalized Linear Models (GLMs). We used a Poisson distribution for count data using CTS from both sample designs, but a Negative Binomial distribution was chosen when overdispersion was detected (Hilbe 2007). For the metric of biomass we used a Gaussian error structure. The number of camera-trapping nights per CTS was specified as an *offset* variable in all models to account for difference in sampling effort (i.e. number active nights) between CT deployments.

We controlled for high levels of variable inter-dependence by performing a Pearson's correlation matrix, retaining non-correlated variables ($r < 0.70$). We retained 11 variables describing the local habitat, season, landscape context, and level of human disturbance of CTS sites (vz1k, vzdist, elev, waterlevel, riverdist, defor1k, defor5k, defordist, ctydist, popcomm1 and commdist1; see description of these variables in Table 2). For those variables representing the same class of human disturbance (e.g. deforestation area), the appropriate buffer size was determined by running all models using different buffer thresholds, and then using the threshold resulting in the strongest effect on our response variables. We mitigated for collinearity between the predictors using the Variance Inflation Factor (VIF < 3), excluding the variables above this threshold. We used Akaike's Information Criteria (AICc) to select the models that best fit the data, employing a stepwise method starting with the full model and discarding predictors until we reached a model with the lowest AICc value.

Results

On the basis of 10,447 trap-nights, we recorded 4,059 independent detections of 25 terrestrial vertebrate species, including 21 mammals representing 12 families and eight orders and four large-bodied bird species (Table 3). We found clear differences in *terra firme* forest sites in both species richness and abundance between high- and low-water phases (richness: paired $t = 2.552$, $df = 21$, $p = 0.018$; abundance: paired $t = 2.950$, $df = 21$, $p = 0.007$, Fig. 2A, C). During the low-water season, overall abundance was higher in *terra firme* than in *várzea* sites ($t = 2.709$, $df = 48$, $p =$

0.009, Fig. 2 B). Similarly, species richness was higher in *terra firme* sites (18.42 ± 3.11 species) than in adjacent *várzea* sites (14.31 ± 3.00 species; t = 4.748, df = 48, p < 0.001, Fig. 2 D).

At *terra firme* sites, the black agouti (*D. fuliginosa*) was the most common species followed by the brocket deer (*Mazama spp*), pale-winged trumpeter (*P. leucoptera*), razor-billed curassows (*M. tuberosum*) and collared peccaries (*P. tajacu*). The detection rates of these species were higher during the high-water season than during the low-water season, whereas pacas (*C. paca*), jaguars (*P.onca*), giant anteaters (*M. tridactyla*), giant armadillos (*P. maximus*) and tapirs (*T. terrestris*) were more frequently detected during the high-water phase (Fig. 3A). During the low-water season, brocket deer, black agoutis, pacas, pale-winged trumpeter, razor-billed curassows and collared peccaries were more abundant in *terra firme* than in adjacent *várzea* forests, while tapirs, ocelots (*L. pardalis*), pumas (*Puma concolor*) and small tinamous (*Crypturellus spp*) presented higher detection rates in *várzea* (Fig. 3B).

PCoA ordination revealed differences between sample clusters formed by all *terra firme* sites between the high- and low-water phases of the flood pulse, and between *várzea* forests and *terra firme* sites during the low-water phase (Fig. 4A), which was further confirmed by permutation tests (PERMANOVA; F = 3.964, p = 0.002; F = 10.401, p = 0.001, respectively). *Terra firme* sites occupied the largest area in community space during the high-water phase, with both *terra firme* and *várzea* forest sites during the low-water phase occupying subsets of the larger group, and *várzea* sites occupying the smallest area. Additionally, the Procrustes rotation performed with the *terra firme* CTS from sample design two indicated significant differences in ordination space in the multivariate structure of community composition between the high- and low-water phases (R = 0.74, p = 0.007, Fig. 4B).

Generalized linear models (GLMs) revealed that water level was a significant positive predictor of both overall species abundance and the detection rates for three trophic guilds: frugivore-insectivores, granivore-frugivores and carnivores (Fig. 5 A, D, F, G). The size of the nearest local extractive community was associated with higher detection rates for browsers (Fig. 5 J). Likewise, elevation was a positive predictor of detection rates of insectivore-frugivores (Fig. 5 I). The best model for frugivores retained only elevation as a significant negative predictor (Fig. 5 E). The area of *várzea* within a 1000-m buffer around each CTS best explained insectivore detection rates (Fig. 5 L), while distance to the nearest urban center had the opposite effect on our metric of overall vertebrate biomass (Fig. 5 B). The best GLM model explaining overall species richness and the detection rates of frugivore-carnivore and frugivore-browsers failed to retain any significant predictors (Fig. 5 C, H, K).

Discussion

Species richness and seasonal movements between forest types

Our camera-trapping study provides tantalizing evidence that water level governs the distribution of large terrestrial vertebrates in Amazonian pristine forest mosaics. These species appear to exhibit lateral seasonal movements to take advantage of periodic resource availability in extremely productive floodplain forests. In our study area, the swath of floodplain forest is approximately 20 km wide, thereby providing a vast area of highly productive habitat for terrestrial species during the low-water phase.

In general, *terra firme* forest sites were more species-rich than *várzea* forest sites, a pattern that conforms with results from previous studies comparing assemblages of all mammals, primates, bats, birds and small mammals in Amazonian seasonally-flooded and unflooded forests (Peres 1999, 1997, Haugaasen & Peres 2005b; c; Beja *et al.* 2009; Pereira *et al.* 2009, Bobroweic et al. 2014). Salvador, Clavero & Leite Pitman (2011) reported that floodplain forests in the Peruvian Amazon are more species-rich than *terra firme* forests during the dry season. They also report that the number of species in floodplain forest during the wet season remains the same throughout the year, while in *terra firme*, a sharp increase in species richness coincided with the onset of the wet season. These shifts in the number of species between the two forest types are consistent with our seasonal movement hypothesis, as the bulk of terrestrial vertebrate species likely exit *terra firme* terrains to feed on the seasonally abundant *várzea* forest resources.

Water level represents a physical barrier for most vertebrate species attempting to access *várzea* forests during the high-water phase. This was confirmed by the positive relationship between water level and aggregate community-wide abundance, and the number of detection events of frugivore-insectivores, granivore-frugivores and carnivores. Bobrowiec *et al.* (2014) noted that the flood pulse constituted a physical barrier even for Phyllostomid bats, whose species composition differed between *terra firme* and *várzea* forests during the high-water period, but this effect did not persist year-round. We found clear differences in species composition between *terra firme* and *várzea* forests during the low-water phase and within our *terra firme* samples between the high- and low-water phases of the annual cycle. These results imply that forest fauna can exhibit ephemeral occupancy of *várzea* sites during the dry season and that the rising flood waters force several species to seek suitable habitats in upland forests. These seasonal lateral movements drive differences in species richness and composition between both seasons and forest types.

Food availability and its distribution within forest habitats, is the most important variable explaining the occupancy and abundance of mammals in different forest types (Mendes Pontes, 2004; Haugaasen & Peres, 2007). In *terra firme* forests, fruit production occurs during the early wet season whereas in *várzea* forests, fruit production starts during the late wet season (Hawes & Peres, 2016). A substantial proportion of the large terrestrial fauna may therefore move between *várzea* and *terra firme* forests to exploit seasonally available resources. For instance, frugivore species in our models exhibited a negative abundance relationship with terrain elevation. This predictor can be used to distinguish both forest types, as our *terra firme* CTS were on average situated on terrains 14 m higher than our *várzea* CTS (t-value = 9.458, df = 277, p-value < 0.001). As water levels recede, the terrestrial fauna rapidly colonize *várzea* forests to forage on the seasonal production of residual fruit- and seed-fall (total production minus dispersal and consumption by arboreal frugivores), which can be twice as high as in adjacent *terra firme* forests during this period (Bodmer, 1990). Ungulate species such as collared peccaries and brocket deer exhibit a marked dietary shift following the flood pulse, consuming more fruits in seasonally-flooded forests during the low-water period compared to the high water period (Bodmer 1990).

Water level is an important determinant of species detection rates in highly heterogeneous forest landscapes subjected to marked seasonal floods (Negrões et al., 2011; De Lázari et al., 2013). Haugaasen & Peres (2007) reported three different strategies of landscape movements across forest types, which were reflected in our results: wide-ranging species, year-round residents and interface species. Large-bodied granivore-frugivores such as the large-group-living white-lipped peccaries is a wide-ranging “landscape” species that, on a seasonal basis, occupies large home ranges in different forest types and shift their diets and habitat use in response to both seasonal flooding and resulting resource fluctuations (Bodmer, 1990; Fragoso, 1998; Keuroghlian, Eaton & Desbiez, 2009). Large-bodied myrmecophages and insectivore-frugivores such as giant anteaters and armadillos exhibited low detection rates in *várzea* forests, likely because they are year-round residents in *terra firme* forests. They seldom move between forest types because the permanently wet *várzea* soils preclude their fossorial foraging behavior. We never observed giant armadillo (*P. maximus*) holes in *várzea* forests, but commonly observed them in *terra firme* forests, and this is consistent with previous studies in the Araguaia River (Negrões *et al.* 2011) and Peruvian floodplain forests (Salvador, Clavero & Leite Pitman 2011).

Detection rates of carnivores increased with the water level, a pattern that can be explained by their swimming and climbing abilities, which allow them to both move between temporary forest islands and utilize the tree canopy as floodwaters rose. Jaguars (*P. onca*) in *várzea* forests in the lower Japurá River are known to spend the entire high-water season high up in the trees (E.E. Ramalho, pers. comm.) and subsist upon arboreal and semi-aquatic species such as howler monkeys (*Alouatta seniculus* (Linnaeus, 1766)), sloths (*Bradypus variegatus*, Schinz, 1825) and spectacled and black caimans (*Caiman crocodilus* (Linnaeus, 1758), and *Melanosuchus niger* (Spix, 1825)) (Ramalho 2006).

Conservation implications

Our research supports the existing body of evidence that the Médio Juruá region, and many other regions of the lowland neotropics, should be viewed as an essentially interconnected multi-habitat socio-ecological system. The massive long-lasting seasonal flood pulse (Junk, Bayley & Sparks, 1989) and the associated phenological (Hawes & Peres, 2016), hydrological, ecological (Hawes et al., 2012) and livelihood impacts this engenders (Endo, Peres & Haugaasen, 2016) require conservation planning at the scale of the entire landscape, with major drainage basins representing complementary management units.

Amazonian freshwater ecosystems such as seasonally white-water flooded forests are vulnerable to anthropogenic disturbance. *Várzea* and *terra firme* forests function as ecologically integrated and hydrologically interconnected habitats that are seasonally utilized by a suite of mobile species, with terrestrial fauna often relying upon the temporally staggered resources of both habitats. As such, they are threatened by both aquatic and terrestrial anthropogenic activities at the local and regional scales. The immense fluvial transport network of the lowland Amazon makes even remote forests accessible to hunters (Peres & Lake, 2003), making their faunal resources non-excludable, whilst simultaneously difficult to monitor. These institutional governance challenges over vast tracts of forest partly explain why terrestrial hunting management has thus far proved elusive. Amazonian terrestrial fauna may be comparatively robust to anthropogenic threats as they seasonally move short distances, usually do not form large aggregations, and often occupy large areas of structurally intact forest. White lipped peccaries, which range over vast areas and form herds of hundreds of individuals, are a notable exception. Not only are they a highly preferred hunted species, vulnerable to overhunting even under low-offtake scenarios (Abrahams, Peres & Costa, 2017), but they play an important ecological role as natural agents of disturbance in plant community dynamics (Silman, Terborgh & Kiltie, 2003) and re-distributing nutrients and fertilizing upland forests.

The existing protected area network and management policies were created principally to protect terrestrial ecosystems and are therefore not adequate to mitigate the aforementioned impacts. Protected areas also suffer from design, implementation and monitoring deficiencies and their delimitations does not adequately represent or protect the full suite of biotic diversity (Peres & Terborgh, 1995, Albernaz *et al.* 2012, Castello *et al.* 2013). Although a protected area coverage of ~25% gives the impression of extensive conservation management of floodplains, less than 1% of the aggregate area of Amazonian floodplains in Brazil is strictly protected (Albernaz *et al.* 2012). Sustainable development and extractive reserves represent the majority of all protected areas worldwide. Their conservation effectiveness can be compromised by high human population density, the uncertain economic viability of exploitating non-timber resources and a shortfall in available animal protein resulting from depleted game vertebrate populations (Peres, 2011; Terborgh & Peres, 2017), but see Abrahams, Peres & Costa (2017) and Campos-Silva & Peres (2016) for best-case scenarios of terrestrial subsistence hunting and local fisheries management.

We have shown that a substantial part of the large vertebrate fauna modulates their use of different forests types within a highly heterogeneous forest landscape according to the marked seasonality of *várzea* floodplain forests. *Várzea* forests adjacent to major rivers are preferentially settled by Amazonian extractivists seeking reliable access to transport routes, fertile soils and animal protein (Endo, Peres & Haugaasen, 2016). In Amazonian extractive reserves, the forest type within which villages are situated can modulate their livelihood strategies. Communities with greater access to *terra firme* forests are inherently more agricultural, while communities with greater access to seasonally-flooded forests rely more heavily on the seasonal extraction of non-timber resources such as palm fruits (*Euterpe spp.*, Martius 1824 and *Astrocaryum aculeatum*, Meyer), rubber (*Heavea spp.*, Aublet) and oil seeds (*Carapa guianensis*, Aublet and *Astrocaryum murumuru*, Mart.) (Newton, Endo & Peres 2011).

Our research occupies the confluence between the issues of landscape-scale conservation planning, ecological connectivity, nutrient transport and uptake, and community-based natural resource management. The Médio Juruá region exemplifies these issues as it encompasses extensive seasonal wetlands and a suite of hunted, seasonally-mobile species. Adequate conservation strategies in this region must account for the full life-history needs of mobile harvested species, ecologically interconnected habitats and the diverse livelihood portfolios of local communities (Lindenmayer et al., 2008). Different Amazonian forest types exhibiting staggered resource pulses must be included within the same or neighboring sustainable-use protected areas. This will provide sufficiently large areas to both support large-scale ecological processes (e.g. species migrations, lateral movements, persistence of apex predators) and anthropogenic extractive activities in the long run (e.g. estimated sustainable harvest area for tapir populations >2,000 km^2) (Peres & Terborgh, 1995; Peres, 2001, 2005; Haugaasen & Peres, 2007). This concept can be applicable to conservation planning of other regions consisting of natural forests mosaics experiencing seasonal floods such as the hyper-fragmented region of the Araguaia River or at the Pantanal floodplains (Negrões et al., 2011; De Lázari et al., 2013). In these different scenarios, private reserves must be situated adjacent to protected areas to ensure terrestrial fauna protection during the prolonged inundation season.

Study limitations

In our study, we were unable to estimate the species richness in *várzea* forests during the high-water phase of the flood pulse, because our camera trapping method focused only on terrestrial species, which are more sensitive to the flood pulse than arboreal and semi-aquatic species. *Várzea* forests along this section of the Juruá River are typically subjected to an annual flood pulse amplitude of 8 to 12 m, which lasts for up to six months. Any camera traps deployed in várzea forests during the high-water period would need to be placed almost half way up into the forest canopy.

We acknowledge that these landscape-scale seasonal movements between forest types can only be conclusively verified by either radio or GPS telemetry studies targeting multiple species. The prohibitive costs of such an undertaking limit its community-wide feasibility. Our evidence is based on patterns of local population abundance, species richness and biomass, particularly along the *várzea - terra firme* interface, where temporary overcrowding is expected to occur for species abandoning the wide belt of *várzea* forest during the rise of floodwaters.

Conclusions

The annual floodwaters along several major white-water rivers in the Amazon is the main factor structuring and differentiating *várzea* floodplains from adjacent *terra firme* forests as unique adaptations are required to tolerate the prolonged flood pulse. This remarkable natural phenomenon drives several key ecological processes, including staggered plant phenology, high plant productivity, and supports major local livelihood activities such as subsistence fishing and hunting. This landscape scale seasonal dynamics between these major adjacent forest types was investigated in terms of species richness, species composition and population abundance for as many as 25 vertebrate species. We have shown that many upland forest terrestrial vertebrate species make seasonal use of *várzea* forests to take advantage of the abundant trophic resource in this forest type following the receding waters. We acknowledge that detailed movement data using GPS telemetry can further clarify the magnitude and seasonal importance of *várzea* habitat use by *terra firme* vertebrates. However, we highlight that this unique seasonal dynamic is a critical issue in Amazonian forest reserve design and biodiversity monitoring, particularly within large sustainable use reserves encompassing complex natural landscape mosaics, where unimpeded lateral movements should continue to support both local extractive economies and healthy wildlife populations.

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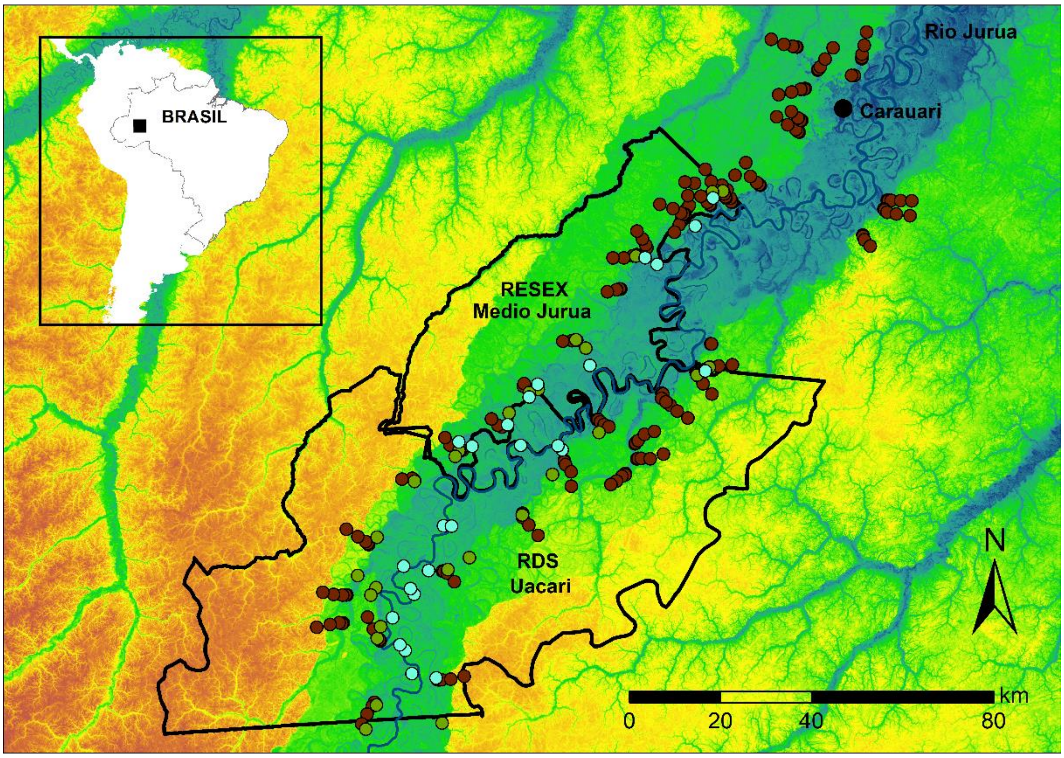
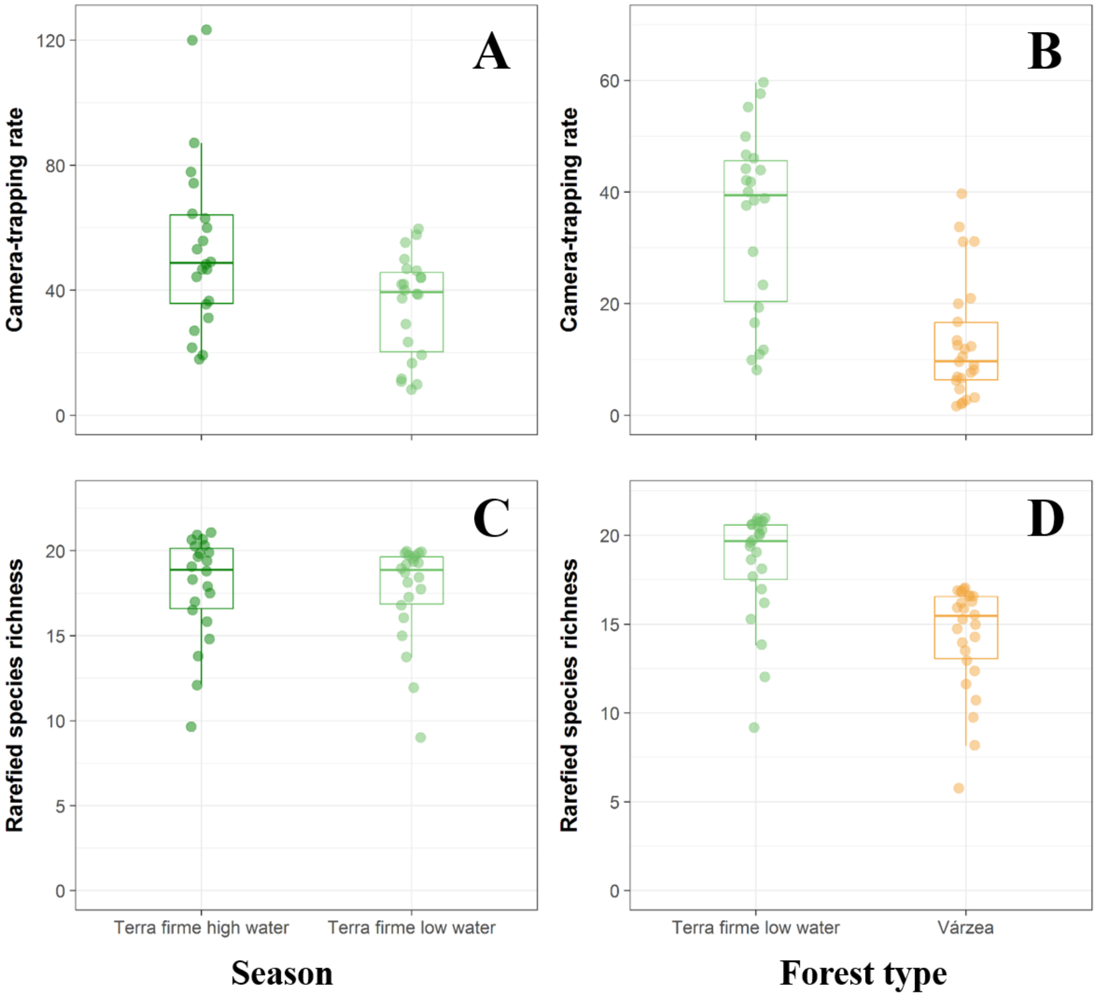
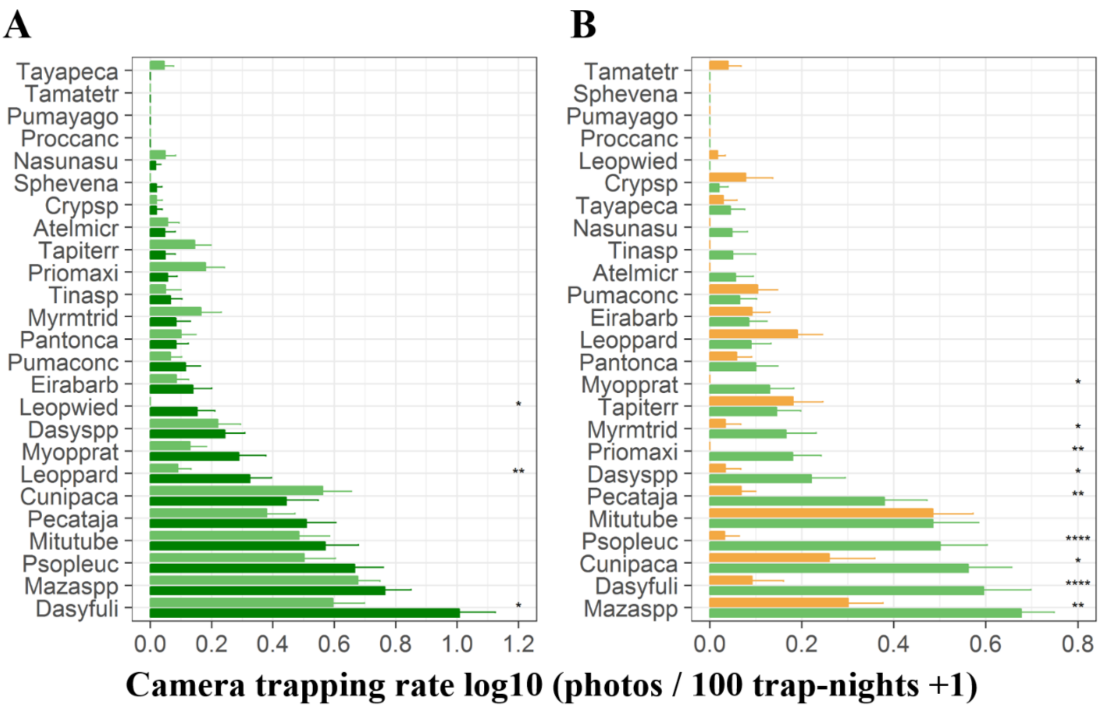


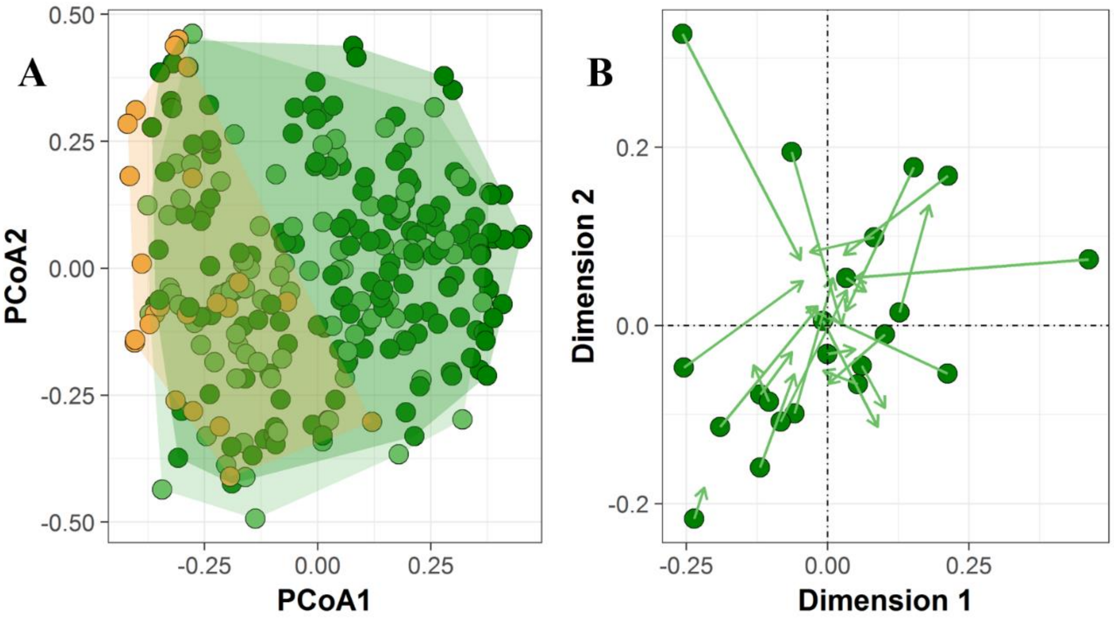
Map of the study area in the central Rio Juruá region of western Brazilian Amazonia, Amazonas, Brazil. Map inset shows the geographic location of the study region (black square). The boundaries of the RESEX Médio Juruá and RDS Uacari are outlined in black. Background colors represent elevation, with blue and brownish orange shades indicating low and high elevation, respectively. Solid red circles represent camera trap stations (CTS) deployed radiating inland into *terra firme* forest (sample design 1). Green and aqua circles represent CTS deployed at *terra firme* forest sites near forest habitat boundaries along the *várzea* interface and far into *várzea* forest, respectively (sample design 2).



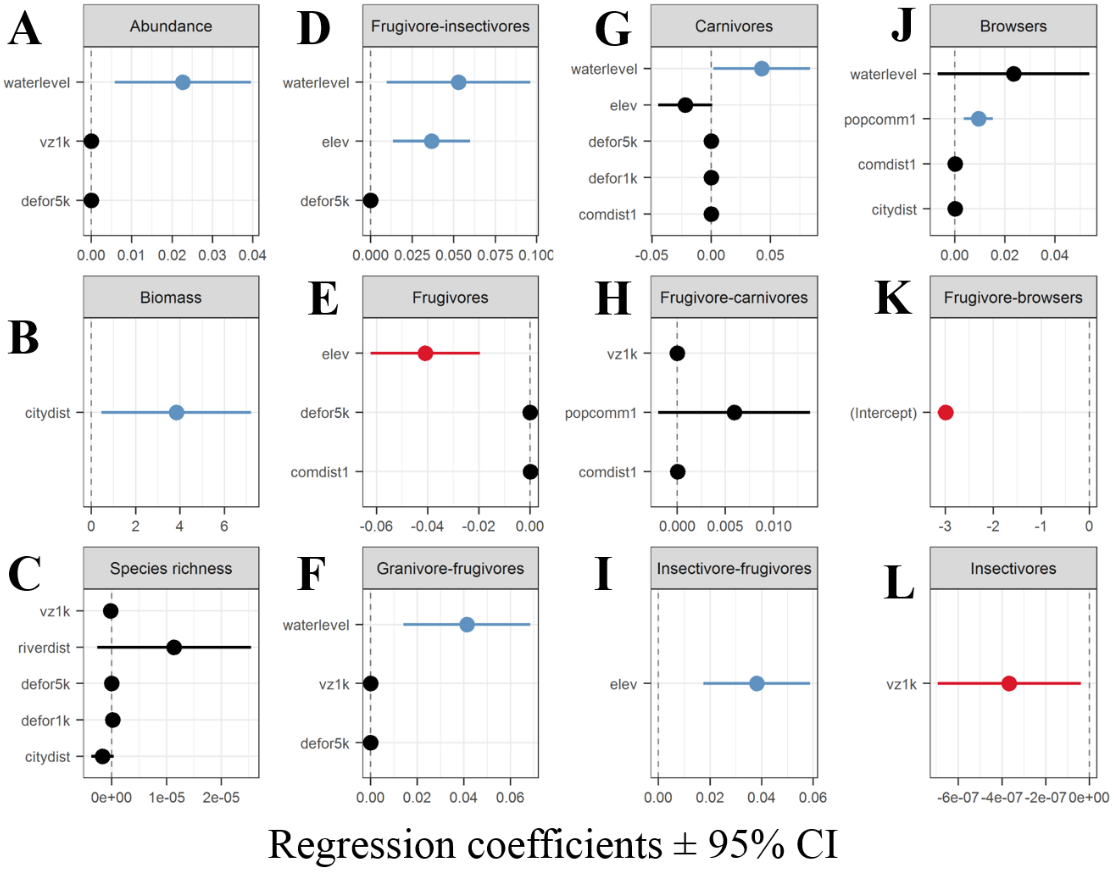
Comparison between *terra fime* and *várzea* forests during both the high- and low-water phases of the flood pulse considering both the total abundance and species richness of terrestrial forest vertebrates. Boxplots comparing abundance and rarefied species richness between *terra firme* forests during both high- (dark green) and low-water (light green) phases of the flood pulse (A and C) and between *várzea* (orange) and *terra firme* forests (light green) during the low-water phase (B and D).



Camera trapping rate of terrestrial vertebrates recorded in *terra firme* and *várzea* forests. (A) Camera trapping rates in *terra firme* forests during both high- (dark green bars) and low-water phase of the flood pulse (light green bars). (B) Camera trapping rates in both *terra fime* and in *várzea* forests during the low-water phase of the flood pulse. Light green and orange bars represent *terra firme* and *várzea* forests, respectively. Species are represented by the first four letters of each genus and first four letters of each species and ordered from least to most abundant top to bottom. Asterisks indicate significant differences according to paired (A) and unpaired t-tests (B); *$p \leqslant 0.05$, **$p \leqslant 0.01$, *** $p \leqslant 0.001$.



Terrestrial vertebrate species composition in Amazonian seasonally-flooded and unflooded forests during both high- and low-water phases of the flood pulse. (A) Principal Coordinates Analysis (PCoA) ordination of the terrestrial vertebrate assemblage structure detected by camera traps in Amazonian *terra firme* forests during both high- and low-water phases of the flood pulse (green and light-green circles, respectively) and in *várzea* forests (orange circles). (B) Procrustes rotation plot of *terra firme* sites sampled during both high- and low-water phase of the flood pulse. Arrows (vectors) indicate the species migration in community space from the high- to the low-water season.



Coefficient estimates (± 95% confidence intervals) showing the magnitude and direction of effects of different explanatory variables retained in the best performing GLMs. (A) aggregate abundance, (B) aggregate biomass of all species, (C) species richness (D-L) numbers of detections of each trophic guild.

Table 1. Camera trapping effort at Amazonian flooded and unflooded forests, along the Juruá River, Amazonas, Brazil (see Fig. 1).

Sample Design	**Flood pulse phase**	**Number of active CTS**	
		Terra Firme	***Várzea***
Sample design 1	From high to low water	193	
Sample design 2	High-water	30	-
Sample design 2	Low-water	30	26
Total		**253**	**26**

Table 2. Covariates used to investigate the seasonal dynamics of terrestrial vertebrates in Amazonian flooded and unflooded forests, along the Juruá

Covariate	Abbreviation	Description
Area of *várzea* forest	vz0.5k	Area (m²) of seasonally flooded forest within a 500m circular buffer centered at each CTS
	vz1k	Area (m²) of seasonally flooded forest within a 1000m circular buffer centered at each CTS
	vz5k	Area (m²) of seasonally flooded forest within a 5000m circular buffer centered at each CTS
Distance to *várzea* forest	vzdist	Euclidean distance from each CTS to the nearest várzea forest
Deforestation area	defor0.5k	Total area (m²) of deforestation within a 500m circular buffer centered at each CTS
	defor1k	Total area (m²) of deforestation within a 1000m circular buffer centered at each CTS
	defor5k	Total area (m²) of deforestation within a 5000m circular buffer centered at each CTS
Distance to nearest deforestation	defordist	Euclidean distance from each CTS to the nearest deforestation patch
Community size	popcomm1	Number of residents of the local community nearest each CTS
Distance to local community	commdist1	Euclidean distance from each CTS to the nearest local community
Distance to urban center	citydist	Euclidean distance from each CTS to the nearest urban center
Elevation	elev	Elevation (m) of the CTS above the main channel of the Juruá river.
River distance	riverdist	Distance from each CTS to the midpoint of Juruá river
Water level	waterlevel	Mean daily water level of the Juruá river during the deployment period of each CTS

River region, western Brazilian Amazonia.

Table 3. Terrestrial vertebrate species detected by camera trapping stations (CTS) deployed in this study in Amazonian flooded and unflooded forests, along Juruá river, Amazonas, Brazil.

Class	Order	Species	English vernacular name	Trophic guild
AVES	GRUIFORMES	*Psophia leucoptera* (Spix, 1825)	Pale-winged trumpeter	Frugivore-Insectivore
	STRUTHIONIFORMES	*Crypturellus spp* (Brabourne & Chubb, 1914)	Small tinamous	Granivore-frugivore
	GALLIFORMES	*Tinamus sp* (Hermann, 1783)	Great tinamous	Granivore-frugivore
		Mitu tuberosum (Spix, 1825)	Razor billed curassow	Frugivore
MAMMALIA	CARNIVORA	*Panthera onca* (Linnaeus, 1758)	Jaguar	Carnivore
		Procyon cancrivorus (G.[Baron] Cuvier, 1798)	Crab-eating-racoon	Frugivore-insectivore
		Puma concolor (Linnaeus, 1771)	Puma	Carnivore
		Herpailurus yagouaroundi (É. Geoffroy Saint-Hilaire, 1803)	Jaguarundi	Carnivore
		Leopardus wiedii (Schinz, 1821)	Margay	Carnivore
		Leopardus pardalis (Linnaeus, 1758)	Ocelot	Carnivore
		Speothos venaticus (Lund, 1842)	Bush dog	Carnivore
		Eira barbara (Linnaeus, 1758)	Tayra	Frugivore-Carnivore
		Atelocynus microtis (Sclater, 1883)	Small-eared-dog	Frugivore-Carnivore
		Nasua nasua (Linnaeus, 1766)	Coati	Frugivore-insectivore
	CINGULATA	*Priodontes maximus* (Kerr, 1792)	Giant armadillo	Insectivore-Frugivore

		Dasypus spp (Linnaeus, 1758)	Armadillo	Insectivore-Frugivore

Class	Order	Species	English vernacular name	Trophic guild
MAMMALIA	CETARTIODACTYLA	*Tayassu pecari* (Link, 1795)	White lipped peccary	Granivore-Frugivore
		Pecari tajacu (Linnaeus, 1758)	Collared peccary	Granivore-Frugivore
		Mazama spp (Rafinesque, 1817)	Brocked deer	Browser
	PERISSODACTYLA	*Tapirus terrestris* (Linnaeus, 1758)	Tapir	Browser
	PILOSA	*Tamandua tetradactyla* (Linnaeus, 1758)	Southern tamandua	Insectivore
		Myrmecophaga tridactyla (Linnaeus, 1758)	Giant anteater	Insectivore
	RODENTIA	*Myoprocta pratti* (Pocock, 1913)	Green acouchy	Granivore-frugivore
		Dasyprocta fuliginosa Wagler, 1832	Black agouti	Granivore-frugivore
		Cuniculus paca (Linnaeus, 1766)	Paca	Frugivore-browser

CONCLUSÕES GERAIS

O pulso anual de inundação ao longo dos grandes rios de agua branca na Amazônia é o principal fator na estruturação e diferenciação das comunidades ecológicas entre florestas de terra firme e de várzea, uma vez que adaptações únicas são necessárias para tolerar a prolongada inundação. Este fenômeno natural marcante governa diversos processos ecológicos como a fenologia das plantas, crescimento em diâmetro das árvores, bem como atividades extrativistas como a pesca e a caça. A dinâmica sazonal entre esses dois tipo florestais foi investigada em termos de riqueza e composição de espécies bem como em abundancia populacional de 25 espécies de vertebrados terrestres. Nós demostramos que várias espécies de vertebrados terrestres utilizam a várzea de maneira sazonal atraídas pela abundância de recursos depositados no chão da floresta logo após o recuo das águas. Reconhecemos que dados detalhados de movimento das espécies, adquiridos através de telemetria GPS, podem elucidar com detalhes a magnitude e importância do uso sazonal da várzea por vertebrados de terra firme. Dessa forma salientamos que essa dinâmica sazonal é um fator fundamental para o design e para o monitoramento da biodiversidade em áreas protegidas na Amazônia, particularmente em reservas extrativistas e de desenvolvimento sustentável que englobam complexos mosaicos naturais na paisagem, onde os movimentos laterais da fauna terrestre devem ser garantidos para assegurar tanto os modos de vida extrativistas quanto populações viáveis a longo prazo.

ANEXOS

Anexo 1 - Normas da revista PEER J, na qual foi encaminhado para publicação o capítulo I dessa Dissertação.

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Figure and Table numbering is determined by the system based on the ordering in which it appears on the file upload screen. You can re-order them using drag and drop.

Figures must be organized, and cited for the first time, in ascending numerical order. This means that Figure 1 must be the first figure in the text and be cited first, Figure 2 must be the second figure in the text and be cited for the first time after Figure 1's citation, Figure 3 must be the third figure in the text and be cited for the first time after Figure 2's citation etc.

Figures can be submitted as EPS and PDF (for vector images), or PNG (for lossless images) for initial review. If figures are provided as PDF for initial review, high quality EPS or PNG files must be submitted at revision for use in final publication.

Unnecessary white space should be eliminated around each figure & figure part.

Uniform fonts and font sizes should be used for labels (letter sizing should be readable at ‘actual sized’ reproduction - we suggest a vertical height of 2 mm).

The panels of each multi-part figure should be arranged however the figure is intended to be published and saved in a single file. Each part should be labeled with an uppercase letter for each figure part (e.g. Fig. 3C) and a single number for the whole figure group.

Minimum image size: 900 by 900 pixels.

These requirements ensure appropriate on-screen reproduction at an acceptable size. However, there will also be an opportunity to provide high-resolution versions of your images at revision.

Accepted and preferred file formats
Figures Use the original file format and image size whenever possible.
Vector images
(e.g. charts, diagrams):
PDF (preferred)
EPS
PNG
Raster/bitmap images
(e.g. drawings, screenshots):
PNG (preferred)
JPEG (photographs only)

PDF
EPS
Ideally at least 3000px wide.
Must be over 900px.

Tables

Check your tables with the Figure and Table checks

… can be submitted as .DOC (MS Word), .DOCX (MS Word), .ODT (Open Doc). PDFs may be provided for initial review, text-based source files must be provided at revision for use in final publication.

For clarity, the name of your uploaded files should include "Table 1" "Table 2" etc.

A Verify details button will display next to each file you upload. Please use this button to verify details for every file. This may be as simple as selecting the type of file you have uploaded (manuscript, figure, table etc) or you may be required to enter a title and legend.

The Title is the one sentence title of a figure. Don't include 'Table 1', 'Table 2' etc.
(we will add that for you).

The Legend is the optional several sentence description.

Cite tables in text as 'Table 1', 'Table 2' etc.

Tables must be organized, and cited for the first time, in ascending numerical order. This means that Table 1 must be the first table in the text and be cited first, Table 2 must be the second table in the text and be cited for the first time after Table 1's citation, Table 3 must be the third table in the text and be cited for the first time after Table 2's citation etc.

Include units in column and row headings, in parentheses.

Tables must fit in a single 21.6 x 28 cm page with 2.5 cm margins.

Place footnotes below the table; these may be used to explain abbreviations.

Note that our system allows multiple files to be uploaded at once.

Accepted and preferred file formats

TablesDOCX (preferred), DOC, ODT; PDF for LaTeX users

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Example:

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... since our system cannot convert .tex files, we ask that you upload a PDF that you have generated yourself as the manuscript. Then upload the source tex files as "Latex source files" in the Primary file category.

Data and Materials

All authors are responsible for making materials, code, raw data and associated protocols relevant to the submission available without delay.

Please ensure that all relevant datasets, code, images and information are available in one of the following possible ways and provide a link to the appropriate location: uploaded as Supplemental Files, deposited in a public repository, or hosted in a publicly accessible database. There are very few circumstances in which we can accept a manuscript without raw data (see point 4 in 'Preparing your submission').

Supplemental Information (SI)

... SI files are published as links alongside the article, which point to downloadable files. These files do not form an integral part of the manuscript and may include supplemental information or important data which are too large for inclusion in the main manuscript. As they are provided as ‘original’ files, readers will need to be able to open them using their own resources. Therefore to ensure widest compatibility you should utilize common file types and avoid proprietary formats.

All files should be named as a “Supplemental [Item] S[number]”. Please include a brief descriptive title and legend in the metadata when uploading the file.

In total, all Supplemental Files should not exceed 50 MB (if more space is needed, please contact us). Individual files should not exceed 30 MB.

Note that our system allows multiple files to be uploaded at once.

If it's necessary to cite Supplemental Information files in the text, use the following style: Fig. S1, Table S1, Data S1, Video S1, Article S1, Audio S1.

If the Supplemental Files are only intended for review purposes and cannot be published, please upload the files as review-only info from the drop down menu in the Supplemental Files section.

For maximum compatibility, we suggest that you submit Supplemental Information using the following formats:

Supplemental Figures	Submit as JPG (use maximum quality settings), EPS (for vector images), or PNG (for lossless images).
Supplemental Tables	Submit as PDF, DOC, Excel, RTF or TeX / LaTeX files.

Supplemental Articles	Submit as PDF.

Supplemental VideosSubmit as AVI, MOV, and MP4 files. For widest compatibility, we suggest authors provide video files as 128 kbit/s AAC audio and 480p H.264 video in an MPEG-4 (mp4) format. Regardless of format submitted, authors should double check that their videos open and play in recent versions of both QuickTime and Windows Media Player.

Supplemental Audio Submit as WAV or MP3 files. Please include a legend. Ensure that the files open and play in common audio players such as iTunes or Windows Media Player.

Large Supplemental Data sets	Submit in a compressed format (e.g. zip or tar.gz).

Style Considerations

Units, Symbols, Mathematics, Abbreviations

Where possible and appropriate, use the International System of Units.

Use discipline specific (non-SI) units only where they are widely adopted within the field.

Symbols should be used in lieu of abbreviations for mathematical expressions & defined at first use.

Spell out the numbers 1-9 unless used with units.

Manuscript Text

Submissions which will result in a final typeset manuscript of 45 pages or more will incur an additional service charge to cover production costs. If you have a manuscript of this extent then please email editor@peerj.com to discuss.

Articles must be written in clear, unambiguous English for an international audience.

The established norms of academic writing within your field should be followed.

Either English or American spelling is acceptable provided it is consistently used throughout.

Nomenclature: Biological & medical nomenclature should adhere to recognized guidelines set forth by international committee regulations or authoritative bodies for specific fields, as applicable.

Tables

Table text should be roman black text.

Special significance can be placed on certain values in the table (e.g., p-values) by bolding, italicizing or underlining the text. Explain in the table legend what the formatting represents.

Figures

Image Manipulation: Figures should only be (minimally) processed or manipulated in order to add labels, arrows, or to change contrast or brightness if applied to the entire image as well as the controls. They should not be adjusted in any way that could lead to misinterpretation of the information in the original image. Unprocessed figure files and data must be retained for editorial review upon request. The descriptions of changes, hardware and software used to take images and make adjustments must also be provided. Inappropriate figure manipulation is grounds for article retraction and/or reporting to institutional oversight boards.

Electrophoretic gels and blots: The display of cropped gels and blots in the manuscript is acceptable if it improves its clarity. In such cases, full-length gels and blots are required in supplementary information at the submission stage.

"Figure" refers to all images such as graphs, charts, line drawings and photographs. When citing figures in the text, the abbreviation "Fig." should be used. If the citation is the beginning of the sentence, use the full word "Figure" instead.

All figures must be cited in the main text.

Ideally legends should not be included in your image files. However legends in images are accepted for initial review, when the legend is placed below the image. For revisions, legends in images are not accepted. Non-LaTeX submissions require legends to be entered manually using the 'Details needed’ button, and should not be included in the manuscript text.

Figure legends should be self contained and clearly describe the figure and its contents.

The graphical area of a figure should include information about scales, abbreviations, limits, etc.

When submitting photographs as figures please indicate the identity of the photographer. If the photographer is not one of the co-authors, please upload a supplemental document with permission from the photographer allowing you to publish the image under a CC BY license.

If you use a map as a figure please cite the source of the map. Wherever possible, use map services which allow unrestricted re-use. If you must use Google Earth or Google Maps then in order to accurately attribute a map from Google, we need to know the third-party data providers cited with the map: find out how.

When creating figures and images consider the accessibility of your chosen color schemes to those with non-normal color vision. Wherever possible avoid using color alone to distinguish between parts of images. When color is used, we suggest that you consult the following resources to ensure maximum accessibility: J*FLY, Mapbox and ColorBrewer.

Linnean Binomials

Authors are encouraged to provide taxonomic authors of Linnean binomials when first used in the text, particularly for taxa that are the focus of the paper in question. Where several taxa are named, citation of taxonomic authors in Tables is regarded as an adequate substitute for citation in the body of the text. Authors of zoological names should consist of initials plus full surnames, whereas authors of botanical names should be abbreviated following Brummitt & Powell's (1992) 'Authors of plant names'. In either case, binomials carrying more than three authors should be abbreviated to 'et al.' subsequent to the name of the third author.

Species formatting

When a species is first mentioned, write out the full name (i.e., genus followed by species):

Use both the genus and species name (e.g., Felis catus).

Italicize the whole name.

Capitalize only the genus name.

The next time that species is mentioned, abbreviate the name (i.e., the first letter of the genus followed by a period and the species), unless:

There are two species that belong to different genera that nevertheless start with the same letter (e.g., Leopardus pardalis, the ocelot, and Lynx canadensis, the Canada lynx). Do not abbreviate the genus name.

There are multiple species with the same species name, but different genera (e.g., Trigonopterus attenboroughi, a beetle, and Prethopalpus attenboroughi, a spider). You can refer to the species by just the genus name, or write the species name in full.

There are two or more species that are are being compared in the same sentence. In this case, you can refer to the species by just the genus name, or write the species name in full.

When you introduce the name of another species in the same genus, you can use the abbreviated genus name for the new species. For example: The domestic cat is species Felis catus. Both F. catus and its wild relative, F. silvestris...

The names of higher taxonomic levels (family, order, class, phylum or division, and kingdom) should be capitalized but not italicized. Common names derived from taxon names, for instance “felines” for members of the family Felidae, should not be capitalized. A common name that is derived from a genus name, such as gorilla, should not be capitalized.