



Universidade Federal de Minas Gerais  
Instituto de Ciências Biológicas  
Programa de Pós Graduação em Ecologia, Conservação e Manejo da Vida Silvestre



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STATUS E DINÂMICA ESPACIAL DE AVES DE SOLO E MAMÍFEROS EM DUAS  
RESERVAS DE DESENVOLVIMENTO SUSTENTÁVEL DA AMAZÔNIA CENTRAL:  
IMPACTO DA CAÇA E DA INTENSIDADE DE INUNDAÇÃO

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DUAS RESERVAS DE DESENVOLVIMENTO SUSTENTÁVEL DA AMAZÔNIA  
CENTRAL: IMPACTO DA CAÇA E DA INTENSIDADE DE INUNDAÇÃO

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## FOLHA DE APROVAÇÃO

"Status e dinâmica espacial de aves de solo e mamíferos em duas reservas de desenvolvimento sustentável da Amazônia  
Central: impacto da caça e da intensidade de inundação"

FERNANDO FERREIRA DE PINHO

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## RESUMO

Neste estudo utilizamos dados de uma extensa amostragem por armadilhas fotográficas em duas Reservas de Desenvolvimento Sustentável (RDS) na Amazônia Central e dados de monitoramentos de longo prazo dos ciclos hidrológicos e da caça para entender como estes fatores podem afetar o status e a dinâmica de vertebrados terrestres. No primeiro capítulo avaliamos como as recentes variações nas intensidades dos pulsos de inundação afetam a dinâmica de aves de solo e mamíferos na RDS Mamirauá. Utilizamos o monitoramento do ciclo hidrológico e dados de armadilhas fotográficas obtidos entre 2013 e 2019 para avaliar como a intensidade das enchentes influencia a colonização, persistência, riqueza e diversidade de aves de solo e mamíferos na RDS Mamirauá. Observamos que as probabilidades de colonização e de persistência de nenhuma espécie foi influenciada pela intensidade da inundação. A riqueza de espécies se manteve estável e a diversidade apresentou baixa variação ao longo dos anos. A adaptação das populações para se manter por até oito meses no estrato arbóreo e a intensidade de inundação mais baixa quando comparada a Amazônia Ocidental, parecem limitar os impactos das variações da intensidade das inundações sobre estas espécies na RDS Mamirauá. No segundo capítulo avaliamos os padrões de coexistência e os impactos da caça em duas espécies de veados do gênero *Mazama* na RDS Amanã. Testamos a hipótese de que em áreas mais sujeitas a caça, *M. nemorivaga* poderia se beneficiar da redução da ocupação por *M. americana*. Utilizamos uma amostragem de 86 sites de armadilhas fotográficas em 2017 e dados de 18 anos de monitoramento de caça para avaliar os padrões de coexistência e como a caça influencia a ocupação e padrões de atividade dos veados. Observamos que *M. americana* são primariamente noturnos, *M. nemorivaga* diurnos e que as espécies se sobrepõem na dimensão espacial do nicho. *M. americana* é caçada com mais frequência do que *M. nemorivaga*, mas a pressão de caça a distâncias maiores que 2,5 km das comunidades humanas parece não afetar a ocupação nem os padrões de atividade das espécies.



Destacamos que as florestas na RDS Amanã são bastante preservadas, uma vez que os habitats convertidos para agricultura e habitação humana representam uma proporção muito pequena do habitat disponível para a fauna silvestre, favorecendo a dinâmica fonte-sumidouro. De forma geral, nossos resultados indicam que a estratégia de conservação da fauna aliada a conservação técnicas de manejo de populações tradicionais tem sido eficaz nas RDSs Mamirauá e Amanã. As baixas densidades humanas, alta produtividade da floresta e alto grau de conservação podem estar permitindo a coexistência da fauna com comunidades humanas. Nossos resultados indicam que as RDSs podem ser um caminho eficaz para a conservação e sustentabilidade na Amazônia Central.

Palavras-chave: Modelo Dinâmico de Comunidades, áreas úmidas, floresta de Várzea, ocupação condicional, padrões de atividade, padrões espaço-temporais, sustentabilidade da caça

## ABSTRACT

In this study, we used a data set from an extensive camera trap survey that was carried out in two Sustainable Development Reserves (SDR), Central Amazonia. In addition, a long-term monitoring of hydrological cycles and hunting was used to understand how these factors could affect terrestrial vertebrate's status and dynamics. In the first chapter, we assess how recent variations in flood pulse intensities affect ground birds and mammals dynamics in Mamirauá SDR. To assess how flood intensity influences the colonization, persistence, richness and diversity of ground birds and mammals in the Mamirauá SDR, we used the monitoring of the hydrological cycle and a camera trap dataset, conducted between 2013 and 2019. We observed that the flood intensity did not influence the probabilities of colonization and persistence of any species. Species richness remained stable and diversity showed low variation over the years. The adaptation of populations to remain for up to eight months in the arboreal stratum and the lower flood intensity when compared to the Western Amazon should limit the impacts of variations in flood intensity on these species in the Mamirauá SDR. In the second chapter, we evaluated the coexistence patterns and hunting impacts of two deer species of the genus *Mazama* in the Amanã SDR. We tested the hypothesis that in areas more susceptible to hunting, *M. nemorivaga* could be favored from reduced occupancy by *M. americana*. To assess coexistence patterns and how hunting influences deer occupancy and activity patterns we used data from 86 camera trap sites in 2017 and data from 18 years of hunting monitoring. We observed that *M. americana* is primarily nocturnal and *M. nemorivaga* diurnal and both species overlap in the spatial dimension of the niche. *M. americana* is more hunted than *M. nemorivaga*, but hunting pressure at distances greater than 2.5 km from human communities does not seem to affect the species' occupancy or activity patterns. We emphasize that the SDR Amanã forests are pristine, since the habitats converted to agriculture and human habitation represent a very small proportion of the habitat available for wildlife, favoring the source-sink

dynamic. Overall, our results indicate that the fauna conservation strategy combined with conservation techniques for managing traditional populations can be effective in the Mamirauá and Amanã SDR's. Low human densities, high forest productivity and high degree of conservation may be allowing the coexistence of the fauna with human communities. Our results indicate that SDR's can be an effective path to conservation and sustainability in Central Amazonia.

Keywords: Dynamic Community Model, wetlands, Várzea forest, conditional occupancy, activity patterns, spatio-temporal patterns, hunting sustainability

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## INTRODUÇÃO GERAL

A Amazônia é a maior e mais biodiversa floresta tropical do planeta, cobrindo uma área que passa de 8 milhões de km<sup>2</sup> (Jenkins, Pimm & Joppa, 2013; RAISG 2009, abrigando mais de 5500 espécies de vertebrados (Da Silva, Rylands & Da Fonseca, 2005) e provendo serviços ecossistêmicos essenciais para o mundo (Fearnside, 2018a; Strand *et al.*, 2018). Apesar de sua reconhecida importância, a pressão antrópica sobre a Amazônia aumentou na última década, com aumento de incêndios não naturais e do desmatamento (Escobar, 2019; INPE, 2021). Outros fatores antrópicos impactam direta e indiretamente a fauna amazônica, por exemplo, quando associada a perda de habitat, a caça reduz as populações de espécies cinegéticas no bioma (Peres, 2001). As projeções climáticas ainda indicam um aumento na frequência de eventos extremos de cheia e seca (Boisier *et al.*, 2015; Gloor *et al.*, 2015) que já tem afetado alguns grupos da fauna em áreas mais sensíveis à grandes variações nos níveis de inundação (Bodmer *et al.*, 2018). Os impactos de eventos extremos sobre a fauna são extremamente preocupantes já que podem diminuir a disponibilidade de caça e pesca e privar a segurança alimentar de comunidades humanas que dependem destes recursos (Endo, Peres & Haugaasen, 2016). Neste cenário, a adoção de estratégias de conservação e promoção de sustentabilidade são essenciais para a manutenção dos serviços ecossistêmicos da Amazônia.

As áreas protegidas representam certamente uma ferramenta importante para a conservação e sustentabilidade (Zafra-Calvo *et al.*, 2019). Somente na Amazônia brasileira, as áreas protegidas cobrem 2.2 milhões de km<sup>2</sup> (Verissimo *et al.*, 2011). Frequentemente, no entanto, a criação de áreas protegidas gera conflitos com comunidades tradicionais que fazem uso da terra, especialmente quando essas comunidades não estão incluídas nos processos de criação (Parente & Burszty, 2012; Anaya & Espírito-Santo, 2018). De fato, neutralizar as atividades insustentáveis e oferecer alternativas que levem a uma melhoria do bem estar humano são os grandes desafios para o desenvolvimento sustentável na Amazônia (Fearnside, 2018b). Neste

sentido, as Reservas de Desenvolvimento Sustentável (RDS) são importantes aliadas para a conservação. O sistema de unidades de conservação do Brasil define as Reservas de Desenvolvimento Sustentável (RDS) como áreas protegidas com o objetivo de preservar a natureza ao mesmo tempo em que assegura qualidade de vida e conserva técnicas de manejo de populações tradicionais (Brasil, 2000). Experiências na Amazônia demonstram que esses objetivos são plenamente executáveis em florestas tropicais (Campos-Silva *et al.*, 2021).

Criada em 1996, a Reserva de Desenvolvimento Sustentável Mamirauá (RDSM) foi a primeira RDS do Brasil (IDSM, 2014). A RDSM surgiu da necessidade de conservar a biodiversidade das florestas das várzeas do Lago Mamirauá e, ao mesmo tempo, promover o bem-estar da população tradicional local (Ayres, 2006). Além de ter sido a primeira RDS implantada no país, a reserva foi extremamente bem sucedida em ações de manejo, mais notadamente no manejo do pirarucu (*Arapaima gigas*), que promove a geração de renda para as comunidades locais e uma recuperação extraordinária das populações da espécie ao longo de 20 anos (Gonçalves, Cunha & Batista, 2018). Dois anos depois da criação da RDSM, a Reserva de Desenvolvimento Sustentável Amanã (RDSA) foi criada com participação decisiva de lideranças comunitárias no Lago Amanã que manifestaram seu desejo da criação da reserva nos moldes da vizinha RDSM (Amazonas, 2020).

A RDSM, localizada na Amazônia Central na confluência dos rios Japurá e Solimões, inunda completamente durante o período de cheia e está completamente inserida em uma área de várzea amazônica, cobrindo 11.240 km<sup>2</sup> (IDSM, 2014). As inundações periódicas decorrem de pulsos de inundação monomodais e previsíveis que resultam em períodos bem definidos de enchente e de seca (Wittmann, Schöngart & Junk, 2010), e são o principal fator de estruturação de comunidades ecológicas nas florestas de várzea (Haugaasen & Peres, 2007; Alvarenga *et al.*, 2018; Ramalho, Machado & Vieira, 2018). A dinâmica das águas associada ao isolamento por dois grandes rios determina a composição de espécies na RDSM. Por exemplo, entre os

mamíferos de médio e grande porte, somente espécies bem adaptadas à hábitos arborícolas parecem residir na RDSM, já que precisam se manter no estrato arbóreo por até oito meses durante a enchente (Alvarenga *et al.*, 2018). A estabilidade e previsibilidade dos pulsos de inundação, no entanto, vem sendo alteradas (Phillips *et al.*, 2009; Cook, Zeng & Yoon, 2012; Boisier *et al.*, 2015; Gloor *et al.*, 2015), e os impactos dessas alterações sobre a fauna são imprevisíveis.

A RDSA, também localizada na região do médio curso do rio Solimões, próximo à confluência com o rio Japurá, é adjacente a RDSM e é uma das maiores áreas protegidas em floresta tropical na América do Sul, com 23.500 km<sup>2</sup> (Amazonas, 2020). No período da cheia, forma-se uma área de floresta inundada (igapó), porém a quantidade de floresta inundada é menor em comparação com a RDSM, compreendendo uma pequena faixa ao longo do perímetro do lago Amanã (Amazonas, 2020). As terras mais altas e que não sofrem as inundações sazonais permitem a ocorrência de mamíferos de médio e grande porte ausentes na RDSM (Alvarenga *et al.*, 2018). Estas espécies são justamente as mais caçadas na RDSA e importantes para promover a segurança alimentar das comunidades humanas locais (Valsecchi & Amaral, 2009), especialmente durante o período de enchente, quando o sucesso de pesca é reduzido (El Bizri *et al.*, 2018). É fundamental entender, portanto, como a caça influencia a ecologia e comportamento das espécies cinegéticas.

O Instituto de Desenvolvimento Mamirauá (IDSM), criado em 1999, desenvolve atividades nas duas reservas desde seus primeiros anos de criação, com a missão de “promover pesquisa científica sobre a biodiversidade, manejo e conservação dos recursos naturais da Amazônia de forma participativa e sustentável” (IDSM, 2021). Ao longo destes vinte anos de gestão participativa com as comunidades ribeirinhas na região do Médio Solimões, o IDSM promove a qualidade de vida através de tecnologias sociais sustentáveis e gera conhecimento científico em diversas áreas através dos seus grupos de pesquisa (IDSM, 2021). Todas as ações do IDSM

são suportadas por conhecimento científico e monitoramento socioambiental para promover o manejo adaptativo. Os produtos desta tese vão de encontro aos objetivos do IDSM ao avaliar o status e tendências da biodiversidade na RDSM e RDSA e promover conhecimento científico para subsidiar planejamentos efetivos de manejo e conservação da biodiversidade na região do Médio Solimões.

Idealmente os indicadores de status e tendências da biodiversidade devem vir de dados primários coletados usando metodologias consistentes e padronizadas (Ahumada, Hurtado & Lizcano, 2013). As armadilhas fotográficas são ferramentas úteis para gerar estes indicadores, já que são facilmente replicáveis e eficientes para monitorar mamíferos e aves de solo (O'Connell, Nichols & Karanth, 2010; Ahumada *et al.*, 2020). Além disso, dados obtidos por armadilhas fotográficas são versáteis para responder perguntas ecológicas em diferentes escalas espaciais e temporais e estão sujeitos a pouca interferência humana (Ahumada *et al.*, 2013). Neste estudo utilizamos dados de uma extensa amostragem por armadilhas fotográficas nas duas RDS na Amazônia Central e dados de monitoramentos de longo prazo de fatores ambientais e antrópicos que potencialmente podem afetar o status e a dinâmica de aves de solo e mamíferos. Dividimos a tese em dois capítulos que abordam fatores relevantes que podem influenciar a fauna na Amazônia: caça e mudanças climáticas.

No primeiro capítulo avaliamos como as recentes variações nas intensidades dos pulsos de inundação ao longo dos últimos anos (2013-2019) afetam a dinâmica de aves de solo e mamíferos na Reserva de Desenvolvimento Sustentável Mamirauá. As intensificações das cheias e secas já têm sido observadas em áreas de várzea e implicado em impactos sobre a fauna (Bodmer *et al.*, 2018) e comunidades humanas (Endo *et al.*, 2016; Tregidgo *et al.*, 2020). A RDSM, no entanto, apresenta características peculiares. Além de ser a maior reserva completamente inundável do Brasil, está localizada na confluência de dois grandes rios que dificultam a dispersão para a maioria das espécies. Diante disso, identificar como essas



variações tem impactado a dinâmica da fauna na RDSM é de extrema relevância para entender os impactos das mudanças climáticas sobre essas comunidades. O IDSM já realiza o monitoramento do ciclo hidrológico na RDSM há mais de 30 anos e o monitoramento da fauna, por meio de protocolo padronizado de armadilhas fotográficas, desde 2013. Utilizamos este extenso banco de dados para avaliar como a intensidade das inundações tem impactado a dinâmica da fauna na RDSM.

No segundo capítulo avaliamos os padrões de coexistência e os impactos da caça em duas espécies de veados do gênero *Mazama* na Reserva de Desenvolvimento Sustentável Amanã. A ideia deste trabalho surgiu após comunitários relatarem a preferência pela caça do veado-vermelho (*Mazama americana*) em relação ao veado-roxo (*M. nemorivaga*) na RDSA. De fato, observamos que a taxa de abates do veado-vermelho é consideravelmente maior no monitoramento de caça realizado pelo IDSM e que esse padrão é registrado em outras partes da Amazônia (Bodmer *et al.*, 1994; Peres, 1997). Apesar disso, a taxa de registros do veado-vermelho por armadilhas fotográficas é consideravelmente maior que a do veado-roxo em nossa área de estudo. Diante disto consideramos a hipótese de que em áreas mais sujeitas a caça, o veado-roxo poderia se beneficiar da redução da ocupação por veados-vermelhos. Entender como a caça influencia a ocorrência e as interações entre as espécies é fundamental para elaborar estratégias efetivas de conservação das espécies cinegéticas sem prejudicar a segurança alimentar das comunidades humanas locais. Utilizamos uma amostragem de 86 sites de armadilhas fotográficas e dados de 18 anos de monitoramento de caça para avaliar os padrões espaciais e temporais na coexistência e caça dos veados.

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## **CHAPTER 1 - Effect of flood pulse intensity on ground birds and mammals in a seasonally flooded Amazonian forest**

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### **Abstract**

Seasonal flood dynamics is the main structuring factor for ecological communities in Amazonian Várzea forests. The current fauna composition and dynamics in Várzea result from adaptations to periodic floods and involve different strategies that require predictability of flood pulses. However, this predictability has been altered by the climate crisis. In this study, we assessed how the intensity of flood pulses influenced the dynamics of ground birds and mammals' populations in Várzea forests in central Amazon over seven years. We used camera traps to survey between 50 and 54 permanent camera trap stations between 2013 and 2019. We used the Dynamic Community Model (DCM) to assess the effect of flood intensity on

colonization and persistence, and estimated overall and subgroup species richness (non-primate mammals, primates, and birds) for each year from the DCM parameters. We also estimated the proportion of sites occupied by each species each year and used these metrics as a proxy of abundance to calculate overall and pairwise abundance similarity over the years. Flood intensity did not influence the colonization and persistence rates of any species. Similarly, overall species richness and subgroup richness were stable across the years, indicating that flood pulse variation did not appear to affect richness. Overall similarity based on abundance was 0.62 with 45% of the variation explained by the balanced variation component and 55% explained by the abundance gradient component. Pairwise similarity between years was always equal to or greater than 0.7, despite variation in flood intensity during the survey period. This study reinforces the indication that community composition of larger mammals and terrestrial birds in the *Várzea* studied is strongly determined by environmental filters imposed by historical pattern of flood pulses. The selection of highly adapted populations and the lower intensity of the flood pulses in relation to the western Amazon seems to limit the impacts of variations in flood intensity on ground birds and mammals in our study area in central Amazon.

Keywords: Dynamic Community Model, colonization, persistence, wetlands, *Várzea* forest

## **Introduction**

Wetlands are defined as areas permanently or seasonally flooded by freshwater, such as floodplains, or coastal and marine areas, such as estuaries, lagoons, mangroves, and reefs, which together cover more than 15 million km<sup>2</sup> worldwide (Davidson and Finlayson 2018). Proportionately, wetlands promote a higher number of ecosystem services, which include availability of water quality, climate change mitigation, health and livelihood, local development, and poverty eradication (Russi et al. 2013). In recognition, more than 2,300



Ramsar Sites, covering nearly 2,500,000 km<sup>2</sup>, were created through international cooperation with the aim of promoting the conservation and rational use of wetlands (Ramsar Convention on Wetlands 2018). Nevertheless, natural wetlands are still declining globally (Ramsar Convention on Wetlands 2018).

Floodplain forests are the main wetlands in the Amazon basin, covering 14% of the region (about 1,000,000 km<sup>2</sup>) (Junk and Piedade 2010). Amazonian seasonally flooded forests were formed in the last glaciation period, about 12,000 years ago, and have been relatively stable for the last 5,000 years (Junk 1993). These forests undergo periodic flooding from monomodal and predictable pulses, resulting in well-defined flood and dry seasons (Wittmann et al. 2010). Flood pulses are critical to ecological processes of seasonally flooded forests, as it controls the biogeochemical cycles and the life cycle of multiple organisms such as algae, macrophytes, trees, fish, and invertebrates (Junk et al. 1989; Junk 1997).

The wetlands along the Amazon basin are characterized by the physical-chemical parameters of the region's main rivers. 'Igapós' are flooded by black, clear, nutrient-poor waters, while 'Várzeas' are flooded by white water rivers exceptionally rich in nutrients, as a result of the high net primary productivity of its adjacent vegetation (Junk 1997; Haugaasen and Peres 2006; Wittmann et al. 2010). Várzeas cover approximately 200,000 km<sup>2</sup> of the Amazon basin (Junk et al. 2010) and in the Solimões/Amazonas complex in central Amazon, their periodic flooding engenders a 10 to 12 meters elevation in the water level every year, reaching its maximum inundation in June-July and its minimum in October-November (Piedade et al. 2000; Ayres 2006).

Topography is determinant to the forest structure in Várzeas, as it is directly related to the flooding level (Junk et al. 1989). Accordingly, Várzea forests are classified into three main types: (1) High Várzea are the highest areas, subjected to shorter flood periods; (2) Low Várzea are areas at lower elevations, subjected to long periods of flooding and; (3) 'Chavascal' are

depressions and oxbows areas permanently waterlogged due to impermeability of the ground layer (Wittmann et al. 2010). Most tree species in Várzeas are restricted to small topographical ranges, which creates a large variation in vegetation composition and structure along the elevation gradient (Parolin 2002; Wittmann et al. 2002). This variation in vegetation structure may be important to determine the distribution of wildlife, however, knowledge about species' habitat use and selection in Várzea forests is scarce.

Seasonal flooding dynamics is the main structuring factor for ecological communities in Várzea forests (Haugaasen and Peres 2007; Beja et al. 2010; Alvarenga et al. 2018; Ramalho et al. 2018). The current composition and dynamics of the wildlife community in Várzea forests result from a long process of adaptation to the periodic flood, which involves different strategies and most likely requires predictability of flood pulses. Movement to higher areas during the wet season by species that are more dependent on terrestrial habitat (Bodmer et al. 2018), as well as species' colonization of Várzeas to take advantage of the high productivity during the dry season (Costa et al. 2018) are strategies adopted to cope with flood pulses in the Amazon. Additionally, birds (Rowedder et al. 2021) and jaguars (*Panthera onca*) (Ramalho et al. 2021) are known to perform vertical migration in floodplain forests during the wet season, occupying higher strata of vegetation when the understory is flooded.

The stability and predictability of flood pulses that allowed such adaptations, however, is being altered by the climate crisis (Bodmer et al. 2018). Climate models for the Amazon basin indicate an increase in the intensity and duration of flooding in the wet season and a decrease in precipitation and water levels in the dry season (Phillips et al. 2009; Cook et al. 2012; Boisier et al. 2015; Gloor et al. 2015). Bodmer et al. (2018) identified a drastic reduction in terrestrial mammals' populations in years of more intense flooding in a western Amazon Várzea. The authors suggest that the reduction was due to the unusual flooding of higher lands that serve as refuge during the flood period, which resulted in increased competition for limited non-flooded

areas and even drowning. In contrast, arboreal species or species with greater swimming ability maintained stable populations even in consecutive years of intense flooding (Bodmer et al. 2018), indicating that the effects of flood pulse intensity on wildlife in Várzea forests may vary according to species composition and local topography. Therefore, a better understanding of how the intensification of hydrological cycles influences Amazon wildlife is of major importance, as it has clear conservation implications and can even affect wildlife use by local human communities (Endo et al. 2016; Tregidgo et al. 2020).

The Mamirauá Sustainable Development Reserve (MSDR), located in the central Amazon, is completely embedded in a Várzea area which is entirely flooded during the wet season (IDSM 2014). In this region, mammal species seem to avoid crossing large rivers, resulting in a significant difference in species composition between the isolated MSDR and its neighboring upland forests (Alvarenga et al. 2018). These conditions seem to have acted as an environmental filter that selected species adapted to survive in the canopy for up to eight months of flooding (Alvarenga et al. 2018). Persistence of wildlife populations under these conditions required morphological, physiological and behavioral adaptations (Coelho 2019; Ramalho et al. 2021), which were driven by the periodicity and predictability of hydrological cycles. Thus, it is expected that even semi-arboreal or good-swimmer species would be influenced by shifts in the historical patterns of flood pulses resulting from the current climate crisis.

Here, we assessed how variation in the intensity of flood pulses over seven years influenced the dynamics of ground birds and mammals populations in the MSDR. We tested the hypothesis that more intense floods would decrease the species' probability of site persistence, whereas less intense floods would increase its probability of site colonization. As flooding can potentially decrease the survival of cubs with reduced mobility, we also tested for a time lag of 2 or 3 years in the estimates of persistence and colonization. Finally, we evaluated the variation

in species richness and diversity of ground birds and mammals over the years. We expected species richness to increase after shorter flooding periods, due to greater possibility of site colonization by species more dependent on terrestrial habitats that would migrate from neighboring upland forests. Likewise, we expected diversity to be more similar between years with similar flooding intensities.

## **Methods**

### *Study area*

The MSDR was created in 1996 and is located in the central Amazon region at the confluence of the Japurá and Solimões rivers, covering an area of 11,240 km<sup>2</sup>. The protected areas system in Brazil defines Sustainable Development Reserves (RDS in Portuguese) as areas dedicated to preserve nature while ensuring quality of life and conserving management techniques for traditional populations (Brasil 2000). MSDR has more than 12,000 residents and users distributed across 212 localities (Moura et al. 2016). The main sources of income in these communities come from government's social programs, fishing, salaries (teachers, health agents, research assistants, environmental protectors and general services) and agriculture (IDSM 2014).

The MSDR is Brazil's largest protected area covering flooded land and is the only one entirely inserted in an Amazonian Várzea area (IDSM 2014). The MSDR landscape can be divided into five main habitat classes: (1) High Várzea has the highest tree species richness among Várzea forests, larger trees, and tolerates flooding lasting 60-120 days/year, (2) Low Várzea has tree species of intermediate size and tolerates flooding of 120-180 days/year; (3) Chavascal is a species-poor, dense forest that grows in terrain depressions; the reduced drainage induces waterlogging of the vegetation cover, even during dry periods, tolerating floods of 180–240

days/year; (4) soil/herbaceous vegetation are transient environments dominated by undergrowth on the edges of water bodies during the dry period and; (5) permanent water includes permanent rivers, canals and lakes (Wittmann et al. 2010; Ferreira-Ferreira et al. 2015).

### *Wildlife survey*

We used between 100 and 108 camera traps (model PC800 HyperFire®, Reconyx Inc, Holmen, Wisconsin, USA) to survey an area of approximately 215 km<sup>2</sup>. Camera trap surveys were carried out annually between 2013 and 2019 in the non-flooded period (September to January), resulting in a total effort of 15,843 camera trap days. Each camera trap station (hereafter referred to as sites) was composed of two camera traps (model PC800 HyperFire®, ReconyxInc, Holmen, Wisconsin, USA) placed 4 m apart, facing each other, and 40 cm above the ground. Each year, we surveyed between 50 and 54 sites for an average of 43 days (Figure 1, Table 1). For logistical reasons, annual surveys were divided into two consecutive blocks, that is, half of the sites were surveyed at first and then all camera traps were relocated to the second block. The survey order of blocks was alternated between years; for example, the block of sites surveyed first in 2013 was the second block to be surveyed in 2014. The average distance from neighboring sites was 1,585 meters, ranging from 876 to 2,725 meters. The area surveyed by camera traps has low human density. Only four communities with a combined population of 289 residents are located less than three kilometers from any of the sites (IDSMS, 2014).

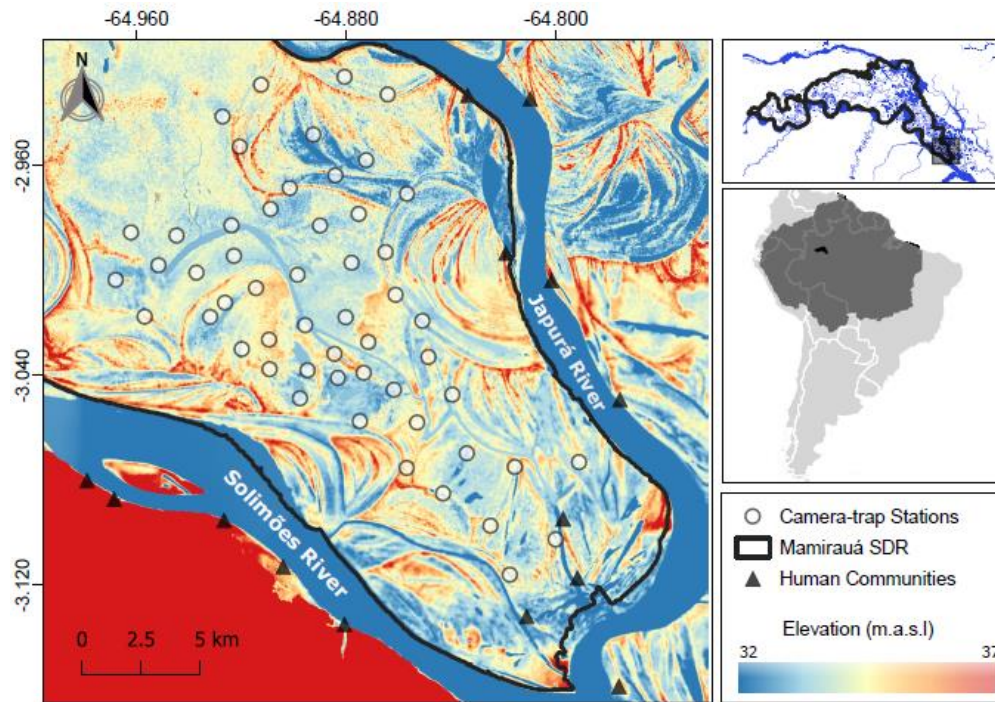


Figure 1 – Camera trap stations surveyed from 2013 to 2019 at Mamirauá SDR. In the upper right map, black line indicates the limits of MSDR and the shaded square represents the sampled area. The South America map shows the location of MSDR (black) within the limits of the Amazon (dark gray).

Table 1 – Camera trap surveys conducted in Mamirauá SDR between 2013 and 2019.

Survey start (YYYY-MM-DD)	Survey end (YYYY-MM-DD)	Total survey effort (days)	Average and range of survey effort per station (days)	Number of survey stations	Number of survey occasions
2013-09-18	2013-12-11	2185	40.46 (38-44)	54	7
2014-09-23	2014-12-23	2284	43.09 (41-44)	53	7
2015-10-31	2016-01-09	1861	34.46 (31-40)	54	6
2016-10-19	2017-01-11	2051	40.22 (30-47)	51	8
2017-09-17	2018-01-14	2909	55.94 (51-59)	52	11
2018-09-16	2018-12-23	2317	46.34 (22-63)	50	10
2019-09-07	2019-12-07	2236	44.72 (40-51)	50	8

### *Covariates*

The classification of habitat classes in the MSDR was previously carried out through remote sensing by Synthetic Aperture Radar (SAR) (Ferreira-Ferreira et al. 2015), which defined five classes described in the study area section. We calculated the proportion of each habitat class in a 250-meter buffer around each site using the *sf* package (Pebesma 2018). We selected only the proportions of permanent water, Chavascal and High Várzea to be included in the analyses, as Low Várzea correlated with other habitats (High Várzea and Chavascal) and the proportion of soil/herbaceous vegetation varies depending on the water level.

We calculated a flood intensity index for each site for each year considering the site's elevation and the river water level in the 365 days (one year), 730 to 365 days (2 years) and 1095 to 730 days (3 years) prior to the end of sampling each year (Figure 2). We calculate the average of the subtraction of daily water level values over the periods defined by the elevation of each site. Higher values of this index indicate longer periods flooded, whereas lowers values indicate the opposite. We used the following formula:

$$\text{floodedIntensity\_1year}[i, t] = \text{mean}(\text{level\_water}[\text{last\_day}:\text{last\_day}-365] - \text{elevation}[i])$$

$$\text{floodedIntensity\_2year}[i, t] = \text{mean}(\text{level\_water}[\text{last\_day}-365:\text{last\_day}-730] - \text{elevation}[i])$$

$$\text{floodedIntensity\_3year}[i, t] = \text{mean}(\text{level\_water}[\text{last\_day}-730:\text{last\_day}-1095] - \text{elevation}[i])$$

Where *i* represents the site, *t* represents the year, and 'last\_day' represents the last sampling day of the year.

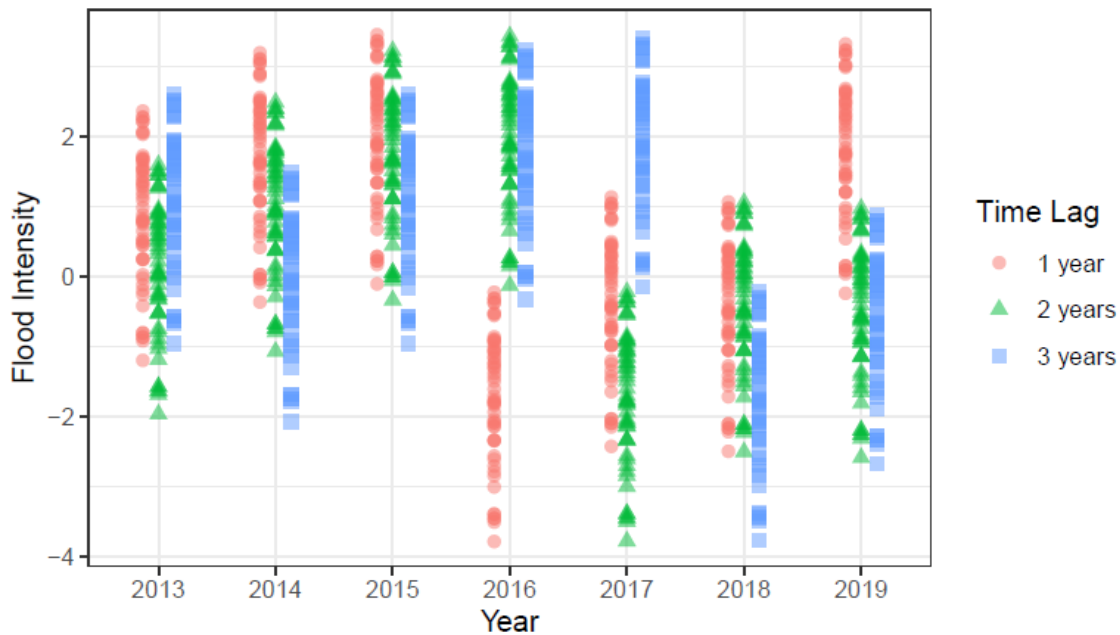


Figure 2 – Flood intensity indices for Mamirauá SDR during the study period. Each tag represents a site and each color a time lag.

We obtained water level data from MSDR’s fluviometric monitoring (IDSMS 2021). Using the *sf* package (Pebesma 2018), we extracted elevation data from the Digital Terrain Model provided by the IDSMS Geospatial Analysis, Environment and Amazonian Territory Research Group. All spatial procedures were carried out in the R software (R Core Team 2021).

In the first two years of survey (2013 and 2014), all sites were baited. As of 2015, only half of the sites were randomly selected to be baited and, thereafter, baited and non-baited sites were alternated between subsequent years. At each baited site, a vented container filled with a mixture of eggs and sardines was placed central to the two camera traps. It allowed the smell to propagate but prevented animals from accessing the food. The presence of bait and the number of days that the camera traps operated in each sampling occasion (ranging from 1 to 7) were entered as detection covariates ( $p$ ) in the occupancy model.



### *Data analysis*

We used camera trap records of all mammal (except small rodents and marsupials not identifiable by camera trap photos) and addition ground birds (orders Eurypygiformes, Galliformes, Gruiformes, Pelecaniformes, and Struthioniformes) for analysis. Each year's survey was divided into occasions of 7 sampling days, resulting in a variation of 6 to 11 survey occasions between years. We constructed a four-dimensional detection/non-detection matrix with 54 sites, 11 survey occasions, 29 species and 7 years. When a site was not surveyed in a year, the line referring to that site was filled with "NA"; as well as the columns referring to occasions without survey, when the number of survey occasions was less than 11.

To assess the effect of flood pulses on colonization or persistence we use the Dynamic Community Model (DCM), an extension of the dynamic occupancy model but for multiple species (Kéry and Royle 2021). The DCM is effective in assessing temporal variation in distribution at both the species and the community levels (Kéry and Royle 2021). Simultaneous modeling of multiple species is beneficial as it synthesizes information from all species, produces improved estimates, and allows for an adequate comparison of species (Zipkin et al. 2010). This approach assumes that the detection, occupancy, colonization, and persistence parameters for each species are extracted from a common distribution governed by hyperparameters that represent the average effect of the covariates over the entire community, which improves the precision of individual species estimates (Kéry and Royle 2016).

The DCM estimates four types of parameters: (1) occupancy ( $\psi$ ) – probability of the species occupying a site; (2) colonization ( $\gamma$ ) – probability of the species occupying a previously unoccupied site; (3) persistence ( $\phi$ ) – probability of a species persisting in a previously occupied site; and (4) detection ( $p$ ) – probability of the species being detected given that it occupies the site. We constructed a DCM with the flood intensity covariate in the dynamic

parameters ( $\gamma$  and  $\phi$ ), the habitat covariates in the initial occupancy parameter ( $\psi_1$ ) and sampling covariates in detection parameter ( $p$ ).

The basic structure of the model, where the possible dependencies of each parameter on covariates vary by site ( $i$ ), sampling occasion ( $j$ ), year ( $t$ ) and species ( $k$ ), is as follows:

$$\psi_1[k] \sim \text{propHV}[i] + \text{propCH}[i] + \text{propPW}[i]$$

$$\phi[k] \sim \text{flood}[i,t]$$

$$\gamma[k] \sim \text{flood}[i,t]$$

$$p[k] \sim \text{effort}[i,j,t] + \text{bait}[i];$$

where  $\text{propHV}$ ,  $\text{propCH}$  and  $\text{propPW}$  represent the proportions of High Várzea, Chavascal and permanent water, respectively, in the 250-m buffer around each site;  $\text{flood}$  represents the flood intensity index (higher values indicate more intense floods);  $\text{effort}$  represents the number of days the camera traps were active on each sampling occasion; and  $\text{bait}$  represents the presence/absence of bait in the site (see Supplementary Information 1 for the complete model).

We used the same model structure to evaluate possible time lags (two or three years) in the effects of flood intensity on the dynamic parameters (colonization and persistence). In these time lag models, only the flood intensity index covariate was altered for the indices considering 2 and 3 years prior to each sampling. Therefore, the model was implemented three times with repetition of all input data except the flood intensity index covariate. We used a Bayesian approach to implement all models in JAGS using the JagsUI package (Kellner 2021) in the open-source R (R Core Team 2021). After a burn-in of 20,000 iterations, we run three chains of 120,000 iterations with a thinning rate of 10 and evaluate convergence with the R-hat

statistic. We used flat priors for all estimated parameters and conducted a sensitivity analysis of the priors, which did not indicate any influence of priors on the estimates (Supplementary Information 2). Inferences related to the influence of flood intensity on colonization and persistence were made only for species with 15 or more records in total, which corresponds to 15 species (out of 29 species recorded - Supplementary Information 3). All inferences were based on posterior means and 95% credible intervals (CRI).

To assess the temporal variation in species richness, we used the parameters of the DCM model to estimate general and subgroup richness (non-primate mammals, primates and birds) with 95% CRI, considering imperfect detectability. We considered the set of species recorded on at least one occasion over the seven years of sampling. Multi-species occupancy models can provide robust estimates of species richness as they incorporate imperfect detection (Dorazio and Royle 2005; Tingley et al. 2020). We also estimated the proportion of sites occupied by each species in each year and used this metric as a proxy for abundance to calculate overall dissimilarity and separate the two components of abundance-based dissimilarity: (1) balanced changes in abundance - when the decrease in the population of one species is compensated by the increase in the population of another species; and (2) abundance gradients - when the population of one species changes between years with no changes in populations of other species (Baselga 2013). We also calculated the abundance-based pairwise community similarity between survey years. All dissimilarity analyzes were performed using the betapart package (Baselga et al. 2021) in the software R (R Core Team 2021).

## **Results**

Flood intensity did not influence the colonization ( $\gamma$ ) nor the persistence ( $\phi$ ) of any of the species assessed in any of the tested time lags (Figures 3-4). We present the effects of

habitat classes on initial occupancy and of bait and detection effort on supplementary material (Support Information 4, 5).

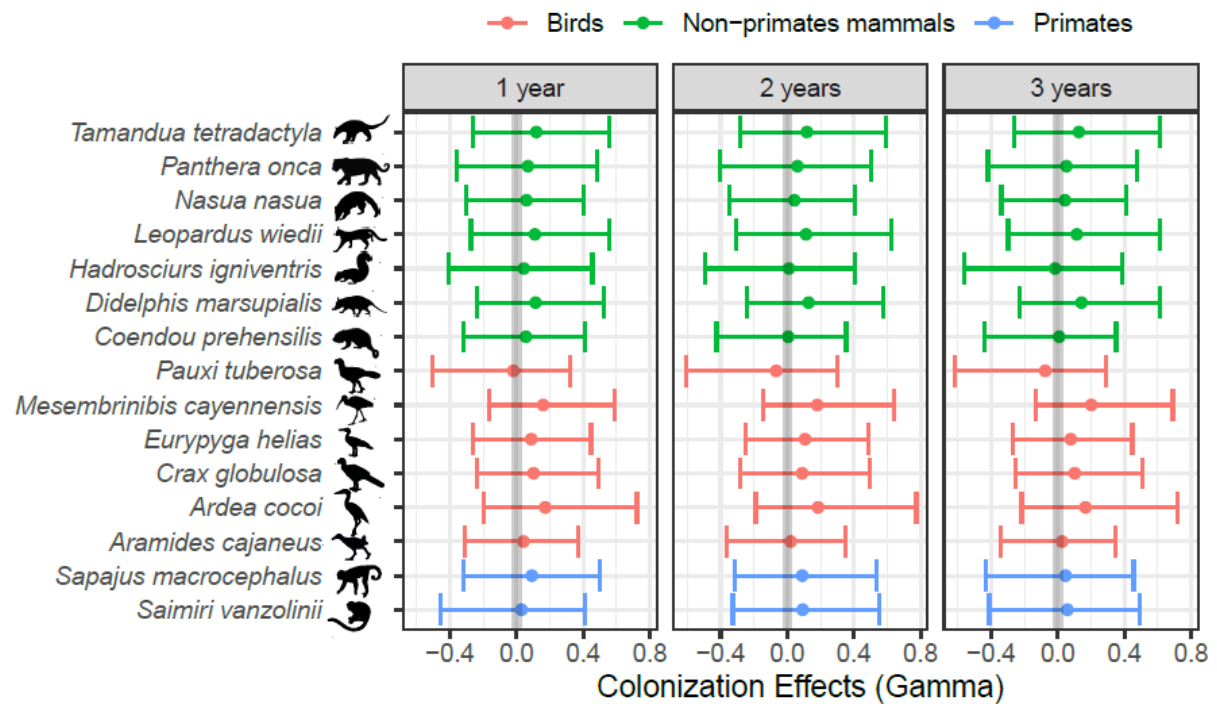


Figure 3 – Mean and 95% CRI of the effect of flood intensity on colonization (gamma) of sites previously unoccupied by the species.

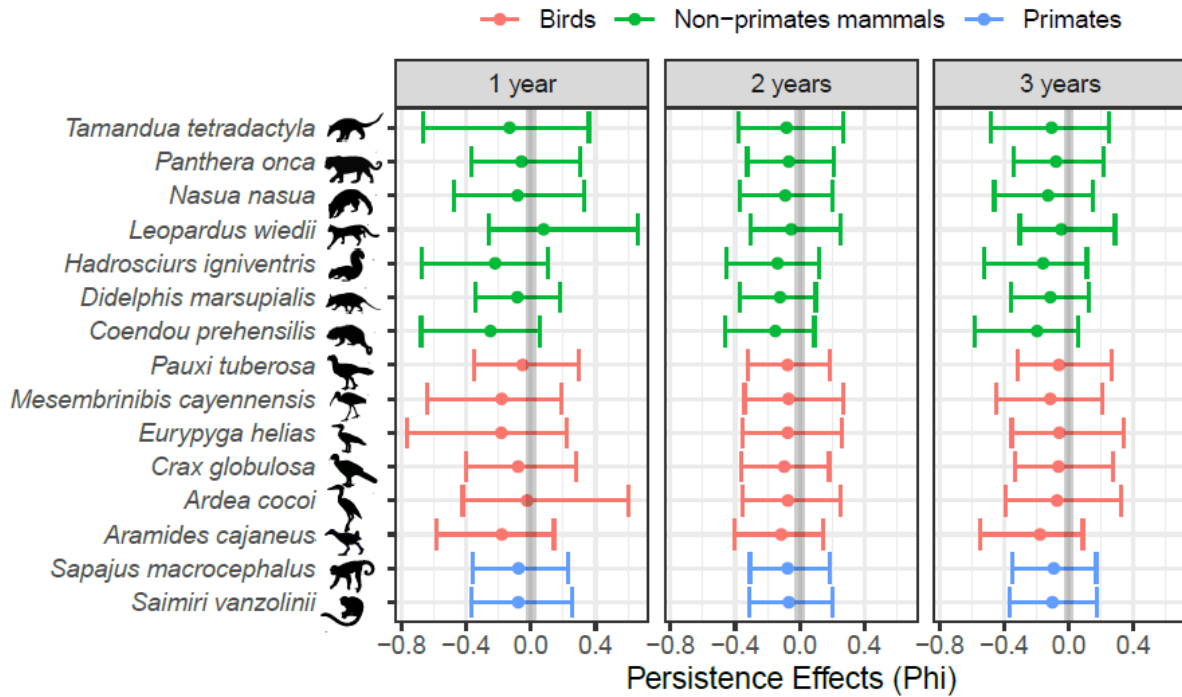


Figure 4 – Mean and 95% CRI of the effect of flood intensity on persistence ( $\phi$ ) in sites previously occupied by the species.

Overall species richness and species richness for each subgroup, did not vary between years, as evidenced by the high overlap of 95% CRI and therefore does not appear to be influenced by variation in flood pulses (Figure 5). The overall abundance-based similarity was 0.62 with 45% of the variation explained by the component of balanced changes in abundance and 55% by the component of abundance gradient. Pairwise similarity between years was always equal to or greater than 0.7 with no indication of less similarity between years with very different flooding intensities (Figure 6).

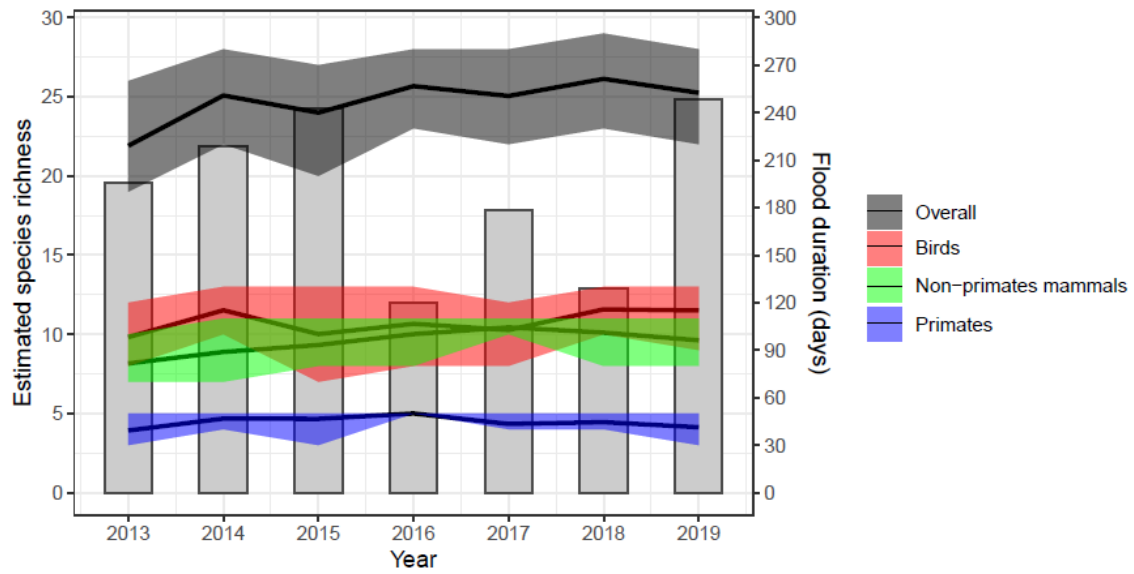


Figure 5 - Estimated species richness and 95% CRI over the years (lines; y-axis on the left) and flood duration in each year (bars; y-axis on the right): number of days the water level was above the average water level during the study (2013-2019) in the 365 days prior to the end of that year's survey.

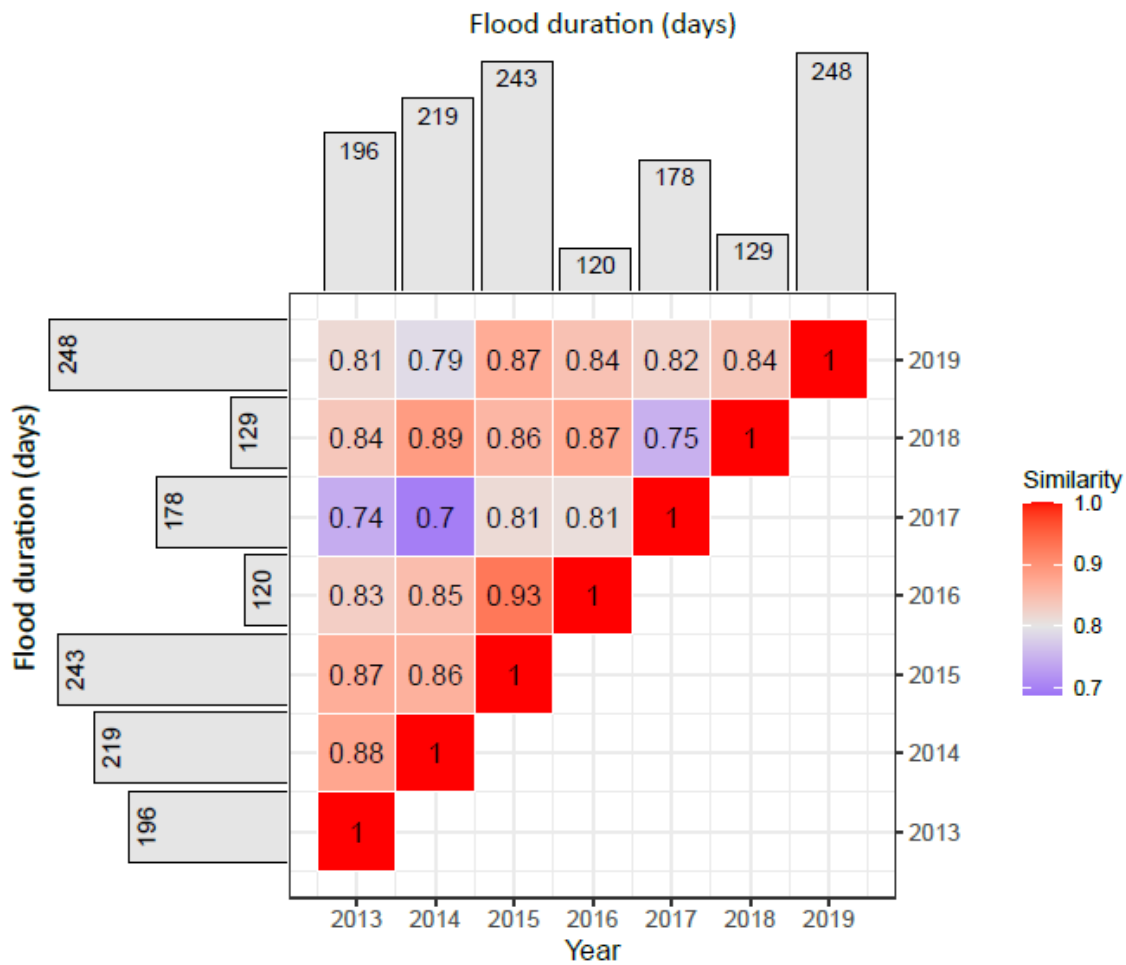


Figure 6 – Pairwise abundance-based similarity between years. Bars on the axes indicate the number of days above the average water level (2013-2019) in the 365 days prior to the end of that year’s survey.

## Discussion

Flooding intensity did not influence the distribution of the terrestrial vertebrates in MSDR. Although intense floods occurred before the surveys in 2015 and 2019 and floods were less intense from 2016 to 2018, this variation did not influence the persistence or the colonization of mammals and ground birds in the study area. Our results are different from those in a Várzea forest in western Amazon, where native mammals populations were drastically reduced after consecutive years of intense flooding (Bodmer et al. 2018). That large block of Várzea forest,

however, appears to have a weaker environmental filter, possibly due to greater connectivity with neighboring upland areas. In fact, population reductions in the western Amazon were observed precisely in species that do not occur or are extremely rare in the MSDR, such as white-lipped peccary (*Tayassu pecari*), collared peccary (*Pecari tajacu*), red brocket deer (*Mazama americana*), black agouti (*Dasyprocta fuliginosa*), lowland paca (*Cuniculus paca*), giant anteater (*Myrmecophaga tridactyla*) and nine-banded armadillo (*Dasypus novemcinctus*). All these species have low capability to use the arboreal stratum, which makes MSDR unsuitable for them during wet season. Furthermore, flood pulses fluctuation in the central Amazon region are smaller than in the western Amazon (Junk et al. 1989; Lamotte 1990). This suggests that Western Amazon may be the first region to suffer the impacts of floods and droughts intensification resulting from the climate crisis.

The periodicity of floods in the MSDR and the isolation imposed by the two major rivers probably drive behavioral adaptations that minimize the effects of more intense flood pulses on the species evaluated here. Ramalho et al. (2021) suggested that the reproductive period of jaguars in the MSDR may be adjusted so that the first months of parental care coincide with the dry season, increasing the probability of cub survival until the next flood season. Little is known about behavioral adaptations of other species in the Várzea. However, the absence of time lag effects in MSDR may indicate that scansorial species, such as South American coati (*Nasua nasua*), Brazilian porcupine (*Coendou prehensilis*) and margay (*Leopardus wiedii*), adopt a similar reproductive strategy, adjusting their reproductive period to maximize offspring survival. The period with available terrestrial habitat in MSDR was shorter in 2015, but its effects were not evident in the probability of colonization or persistence through the following years. The less intense floods in consecutive years (2016-2018) may have contributed to the stability of the species' populations assessed. Morphological adaptations can also be of great importance for maintaining stable populations in Várzea forests. Ramalho et al. (2021)



indicated that jaguars in the MSDR are smaller compared to other populations, which favors its arboreal behavior during the flood. Lizard species (Vitt et al. 2003) and amphibians (Ramalho et al. 2018) also show morphological and behavioral adaptations to survive in flooded forests in the Amazon. These adaptations might be crucial for species that will likely face even more intense hydrological fluctuations in the future; but to what extent even well adapted species could support impacts of the climate crisis impacts remains unclear.

The stability in species richness over the years must be a reflection of the community composition in MSDR, formed largely by species well adapted to flood. Ungulates, medium-sized rodents and armadillos - all species with low capacity to use the arboreal stratum - are frequently recorded in upland neighboring forests (Alvarenga et al. 2018), but are absent or very rare in the MSDR. The ground birds most frequently recorded in our study were from the Cracidae family (*Pauxi tuberosa* and *Crax globulosa*) which, although generally foraging on the ground, are less dependent on the terrestrial stratum, as they also frequently use (Haugaasen and Peres 2008) and build their nests in the arboreal stratum (del Hoyo et al. 2020; Udoye and Schulenberg 2020). In western Amazon, *Tinamus* was the only bird genus that showed reductions in its populations after consecutive years of intense flooding (Bodmer et al. 2018). Possibly due to its high dependence on terrestrial habitat (Haugaasen and Peres 2008), *Tinamus* was never recorded in MSDR throughout the study period. Another tinamid of similar size, *Crypturellus undulatus*, recorded only occasionally by our camera traps, has already been observed crossing the Japurá River towards non-floodable lands during the flood period (Ayres and Marigo 1995 as cited in Cabot et al. 2020). These lateral movements, however, seem unusual in the MSDR.

Isolation by two large rivers limits the movement of most species between neighboring upland forests and the MSDR Várzea. This isolation makes it unfeasible to the MSDR mammal community to adopt the same strategies as in the western Amazon, such as the colonization of

Várzea areas by species more dependent on upland forests during the dry period (Costa et al. 2018). Likewise, isolation limits the movement of species from the floodplains to the higher lands during the flood, to take refuge in non-flooded areas (Bodmer et al. 2018). Isolation seems to restrict even the migration of good swimmers such as the jaguar, which remains in the MSDR even during the flood (Ramalho et al. 2021). In fact, isolation is reflected in the overall low number of records of species most dependent on terrestrial habitats, even though survey was always conducted in the dry season. We highlight, however, that some species highly dependent on non-flooded habitats - white-lipped peccary, puma (*Puma concolor*) and lowland paca - were recorded from 2016 onwards, following a sequence of three years of less intense floods. Those sporadic records were not sufficient to modify species richness estimates, though. Other species highly dependent on non-flooded habitats such as deer, agouti and even the good swimmer tapirs, were not recorded in our study. The limitations to migration from surrounding uplands forests and the capacity of the frequently recorded species to maintain stable populations in our study area may have prevented the number of species from fluctuating over the years.

The same pattern was observed in the similarity estimates based on occupancy (used here as a proxy for abundance). Pairwise similarities between years were always above 0.7 and most often above 0.8, indicating that the community structure remains relatively stable despite wide variation in flood intensity. Given that populations appear to be well adapted to these variations, it is expected that community structure will mirror that stability. The high productivity in Varzeas favors community stability, as it allows species to occur in high abundances (Peres 1997) - already reported in the MSDR for the black squirrel monkey (*Saimiri vanzolinii*) (Paim et al. 2019) and jaguars (Ramalho 2012) - which limits potential cascading effects of stochastic events. In fact, the most relevant component of the community structure variation was the abundance gradient, that is, decreases in occupancy of some species

in some years without similar variation in other species' occupancy. The high habitat quality in MDSR habitats is also likely to be central for the stability in community structure. Although hunting is common in our study area (Lopes et al. 2012; Valsecchi 2012) and usually affects wildlife community structure in the Amazon (Peres 2000), its negative effects in the MDSR is likely to be mitigated by the low human density and the high floodplain productivity. Other relevant threats to wildlife elsewhere in the Amazon, such as habitat loss and forest fires (Barlow et al. 2016; Michalski and Peres 2017; Escobar 2019; INPE 2021), are practically non-existent in our study area.

The composition and structure of the community of ground birds and mammals in the MDSR are highly influenced by the historic environmental filters associated with the annual floods, which profoundly affects the ecological relationships in the Várzea. For instance, competitive release may play an important role in the MDSR community structuring. The margay, a small feline with semi-arboreal habits (Oliveira 1998; Sunkuist and Sunkuist 2002), was frequently recorded in our study area while the ocelot (*Leopardus pardalis*) was never recorded in the seven years of survey. In an upland forest adjacent to the MDSR, ocelots were frequent, while the margay was sporadically recorded (Rocha et al. 2016; Alvarenga et al. 2018). Also, we observed a frequent use of the ground stratum by primates in the MDSR, possibly due to the absence of frugivorous competitors, such as ungulates and medium-sized rodents. Predation relationships are also influenced by flood dynamics. For example, jaguar's diet varies seasonally in the MDSR and is mainly composed of sloths (especially in the wet season) and caimans (during the dry season) (Ramalho et al. 2021). As caimans are more exposed on the margins of rivers and lakes during the dry season, and jaguars share the canopy with sloths in the wet season, that diet adaptation reflects prey accessibility (Rabinowitz and Nottingham 1986; Seymour 1989).

Our findings from 7 years of camera trapping revealed that probability of colonization or persistence for none of the species assessed was influenced by flood intensity. Similarly, species richness remained stable and diversity showed little variation during the study period. This study supports the suggestion that the MSDR's mammals and ground birds fauna is determined by the environmental filter imposed by flood pulses (Alvarenga et al. 2018), limiting the occurrence of species that have no capability to overcome prolonged periods of flood without migrating to upland forests. The few records of species more dependent on non-flooded habitat indicates that colonization of *Várzea* areas during the dry season by species from upland forests, as has been reported for the western Amazon (Costa et al. 2018), seems unusual in the MSDR. Still, these more terrestrial species were recorded during consecutive years of low flooding intensities in our study area. The selection of highly adapted species and the weaker variation in flood pulses when compared to the western Amazon seems to limit the impacts of flood intensity on ground birds and mammals in the MSDR. Our results indicate that, in addition to flood intensity, connectivity to adjacent upland forests may have a strong influence the dynamics of wildlife communities in the Amazonian *Várzea*. In fact, this has important implications for biodiversity conservation in the region considering the projected intensification of extreme events in the Amazon. Besides changes in the availability of the terrestrial stratum, if changes in the connectivity between floodable and non-floodable areas are altered, these extreme events could cause unpredictable changes in wildlife communities of floodplain forests. It is essential therefore to continue monitoring species dynamics in flooded and non-flooded forests with different degrees of connectivity to anticipate the impacts of the climate crisis on wildlife and consequently on local human communities.

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**Supporting Information 1** - R script data preparation and specification of the model used for inference in BUGS language.

```
##### Dynamic occupancy model to evaluate the effects of flood pulse intensity on the
persistence and colonization of ground birds and mammals in the Mamirauá SDR. Adapted
from Kéry & Royle (2021) #####

## Get sample sizes
# y is the detection history arranged in a 4-D array (54 sites, 11 occasions, 7 years, 29
species)
nsites <- dim(y)[1]
nsurveys <- dim(y)[2]
nyears <- dim(y)[3]
nspec <- dim(y)[4]
M=dim(y)[4]

## Covariates
#Initial occupancy:
#propHV is the proportion of High Várzea in a 250 m buffer for each point organized in a
vector (54 sites)
#propCH is the proportion of Chavascal in a 250 m buffer for each point organized in a
vector (54 sites)
#propPW is the proportion of permanent water in a 250 m buffer for each point organized in
a vector (54 sites)

#Colonization and persistence:
# flood is the flood intensity for each site in each year arranged in a site X year matrix (54x7)

#Detection:
# bait is a bait presence/absence matrix for each site in each year organized in a site x year
matrix (54x7)
#effort is the number of days the cameras ran within each seven-day sampling occasion,
organized in a 3-D array (54 sites x 11 occasions x 7 years)

## Bundle and summarize data set
str(bdata <- list(yaug = y, nsites = nsites, nsurveys = nsurveys, nyears = nyears, M = M, effort
= effort , flood = flood, bait=bait, propHV=propHV, propPW=propPW,
propCH=propCH))

# Specify model in BUGS language
cat(file ="model1.txt", "
  model {
    # *** Priors and hyperpriors for model on psi1 ***
    # Priors
    for(k in 1:M){ # Loop over 29 species in augmented list
      alpha.lpsi1[k] ~ dnorm(mu.alpha.lpsi1, tau.alpha.lpsi1)
    }
    for(g in 1:3){ # Loop over 3 coefficients
      beta.lpsi1[g, k] ~ dnorm(mu.beta.lpsi1[g], tau.beta.lpsi1[g])
    }
  }
}
```

```

}
}
# Hyperpriors
mu.alpha.lpsi1 <- logit(mean.alpha.psi1)
mean.alpha.psi1 ~ dunif(0, 1)
tau.alpha.lpsi1 <- pow(sd.alpha.lpsi1, -2)
sd.alpha.lpsi1 ~ dunif(0, 10)
for(g in 1:3){ # Loop over 3 coefficients
mu.beta.lpsi1[g] ~ dnorm(0, 0.1)
tau.beta.lpsi1[g] <- pow(sd.beta.lpsi1[g], -2)
sd.beta.lpsi1[g] ~ dnorm(0, 0.1)I(0,) # Half-Normal prior
}

# *** Priors and hyperpriors for model on phi ***
# Priors
for(k in 1:M){ # Loop over all 29 species
for(t in 1:(nyears-1)){ # Loop over 6 intervals
alpha.lphi[t,k] ~ dnorm(mu.alpha.lphi[t], tau.alpha.lphi) # phi intercept for 6 intervals,
different mean, same variance
}
beta.lphi[k] ~ dnorm(mu.beta.lphi, tau.beta.lphi)
}
# Hyperpriors
for(t in 1:(nyears-1)){ # Loop over 6 intervals
mu.alpha.lphi[t] <- logit(mean.alpha.phi[t])
mean.alpha.phi[t] ~ dunif(0, 1)
}
tau.alpha.lphi <- pow(sd.alpha.lphi, -2)
sd.alpha.lphi ~ dnorm(0, 0.1)I(0,)

mu.beta.lphi ~ dnorm(0, 0.01)
tau.beta.lphi <- pow(sd.beta.lphi, -2)
sd.beta.lphi ~ dnorm(0, 0.1)I(0,)

# *** Priors and hyperpriors for model on gamma ***
# Priors
for(k in 1:M){ # Loop over all 29 species
for(t in 1:(nyears-1)){ # Loop over 6 intervals
alpha.lgamma[t,k] ~ dnorm(mu.alpha.lgamma[t], tau.alpha.lgamma)
# gamma intercept for 6 intervals, different mean, same variance
}
beta.lgamma[k] ~ dnorm(mu.beta.lgamma, tau.beta.lgamma)
}
# Hyperpriors
for(t in 1:(nyears-1)){ # Loop over 6 intervals
mu.alpha.lgamma[t] <- logit(mean.alpha.gamma[t])
mean.alpha.gamma[t] ~ dunif(0, 1)
}

```

```

tau.alpha.lgamma <- pow(sd.alpha.lgamma, -2)
sd.alpha.lgamma ~ dnorm(0, 0.1)I(0,)

mu.beta.lgamma ~ dnorm(0, 0.1)
tau.beta.lgamma <- pow(sd.beta.lgamma, -2)
sd.beta.lgamma ~ dnorm(0, 0.1)I(0,)

# *** Priors and hyperpriors for model on p ***
# Priors
for(k in 1:M){ # Loop over all 29 species
  for(t in 1:nyears){ # Loop over 7 years
    alpha.lp[t,k] ~ dnorm(mu.alpha.lp[t], tau.alpha.lp)
    # p intercept for 7 years, different mean, same variance
  }
  for(g in 1:2){ # Loop over (now) 2 coefficients
    beta.lp[g, k] ~ dnorm(mu.beta.lp[g], tau.beta.lp[g]) # coefs
  }
}

# Hyperpriors
for(t in 1:nyears){ # Loop over 7 years
  mu.alpha.lp[t] <- logit(mean.alpha.p[t])
  mean.alpha.p[t] ~ dunif(0, 1)
}
tau.alpha.lp <- pow(sd.alpha.lp, -2)
sd.alpha.lp ~ dnorm(0, 0.1)I(0,)
for(g in 1:2){ # Loop over 2 coefficients
  mu.beta.lp[g] ~ dnorm(0, 0.1)
  tau.beta.lp[g] <- pow(sd.beta.lp[g], -2)
  sd.beta.lp[g] ~ dnorm(0, 0.1)I(0,)
}

# Likelihood of the model
# Data augmentation submodel
omega ~ dunif(0, 1) # Prior for data augmentation parameter
for(k in 1:M){ # Loop over all 29 species
  w[k] ~ dbern(omega)
}
# Ecological submodel: Define state conditional on parameters
for (i in 1:nsites){ # Loop over 54 sites
  for(k in 1:M){ # Loop over 29 species
    # Initial conditions of system (incl. covariate effects)
    z[i,1, k] ~ dbern(psi1[i, k])
    logit(psi1[i,k]) <- alpha.lpsi1[k] +
    beta.lpsi1[1,k] * propHV[i] + beta.lpsi1[2,k] * propCH[i] + beta.lpsi1[3,k] * propPW[i]

    # State transitions (incl. covariate effects)
    for (t in 2:nyears){ # Loop over years
      z[i,t,k] ~ dbern(z[i,t-1,k]*phi[i,t-1,k] + (1-z[i,t-1, k])*gamma[i,t-1,k])
      logit(phi[i,t-1,k]) <- alpha.lphi[t-1,k] + beta.lphi[k] * flood[i,t]
    }
  }
}

```



```

logit(gamma[i,t-1,k]) <- alpha.lgamma[t-1,k] + beta.lgamma[k] * flood[i,t]
}
}
}

# Observation model (incl. covariate effects)
for (i in 1:nsites){
  for(k in 1:M){
    for (j in 1:nsurveys){
      for (t in 1:nyears){
        yaug[i,j,t,k] ~ dbern(w[k] * z[i,t,k] * p[i,j,t,k])
        logit(p[i,j,t,k]) <- alpha.lp[t,k] +
        beta.lp[1,k] * bait[i,t] + beta.lp[2,k] * effort[i,j,t]
      }
    }
  }
}

# Derived parameters (note multiplication with w)
# Number of occupied sites
for(k in 1:M){
  for (t in 1:nyears){
    n.occ[t, k] <- sum(w[k] * z[,t,k])
  }
}

# Species richness: total and per site/year
Ntotal <- sum(w[]) # Total species richness (community size)
for(i in 1:nsites){
  for(t in 1:nyears){
    for(k in 1:M){
      tmp[i,t,k] <- w[k] * z[i,t,k]
    }
    Nspec[i,t] <- sum(tmp[i,t,]) # Species richness per site and year
  }
}

")

# Initial values (simply initialize all at 1)
zst <- array(1, dim = c(nsites, nyears, M))
wst <- rep(1, M)
inits <- function(){ list(w = wst, z = zst)}

# Parameters monitored
params <- c("omega", "mu.alpha.lpsi1", "sd.alpha.lpsi1",
           "mu.beta.lpsi1", "sd.beta.lpsi1",
           "mu.alpha.lphi", "sd.alpha.lphi",
           "mu.beta.lphi", "sd.beta.lphi",

```

```
"mu.alpha.lgamma", "sd.alpha.lgamma",  
"mu.beta.lgamma", "sd.beta.lgamma",  
"mu.alpha.lp", "sd.alpha.lp",  
"mu.beta.lp", "sd.beta.lp",  
"alpha.lpsi1", "beta.lpsi1",  
"alpha.lphi", "beta.lphi",  
"alpha.lgamma", "beta.lgamma",  
"alpha.lp", "beta.lp",  
"Ntotal", "Nspec", "n.occ", 'z')
```

```
# MCMC settings
```

```
na <- 1000 ; ni <- 120000 ; nt <- 50 ; nb <- 20000 ; nc <- 3
```

```
library(jagsUI)
```

```
out <- jags(bdata, inits, params, "model1.txt", n.adapt = na, n.chains = nc, n.thin = nt, n.iter =  
ni, n.burnin = nb, parallel = T)
```

**Supporting Information 2** - Prior sensitivity analysis by running the model used for species-level inference with three variations of prior specification for the hyper-parameters (common distribution governing the species-specific effects).

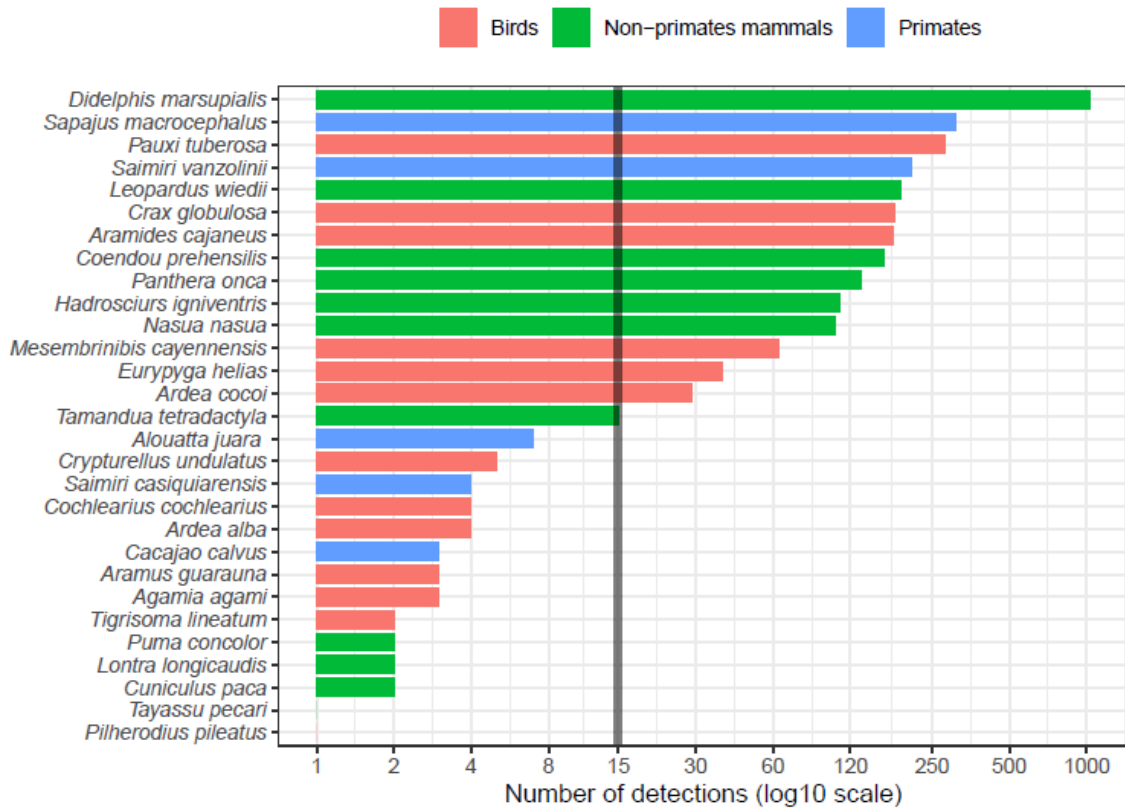
	<b>Model 1</b>		<b>Model 2</b>		<b>Model 3</b>	
	mean	sd	mean	sd	mean	sd
mu.beta.lpsi1[1]	0.026	0.176	0.025	0.176	0.027	0.178
mu.beta.lpsi1[2]	-0.167	0.229	-0.163	0.233	-0.167	0.235
mu.beta.lpsi1[3]	-0.097	0.191	-0.097	0.185	-0.097	0.191
sd.beta.lpsi1[1]	0.278	0.211	0.277	0.204	0.282	0.209
sd.beta.lpsi1[2]	0.551	0.282	0.558	0.281	0.556	0.293
sd.beta.lpsi1[3]	0.300	0.240	0.302	0.245	0.317	0.269
mu.beta.lphi	-0.139	0.125	-0.127	0.115	-0.138	0.124
sd.beta.lphi	0.196	0.160	0.189	0.140	0.206	0.166
mu.beta.lgamma	0.085	0.117	0.081	0.115	0.083	0.114
sd.beta.lgamma	0.146	0.107	0.140	0.107	0.142	0.107
mu.beta.lp[1]	-0.268	0.174	-0.270	0.175	-0.266	0.175
mu.beta.lp[2]	0.438	0.187	0.437	0.193	0.438	0.188
sd.beta.lp[1]	0.608	0.142	0.605	0.141	0.607	0.142
sd.beta.lp[2]	0.652	0.172	0.652	0.171	0.655	0.169

Model 1:  $\mu.\text{beta} \sim \text{dnorm}(0, 0.1)$ ;  $\text{sd}.\text{beta} \sim \text{dnorm}(0, 0.1)I(0,)$

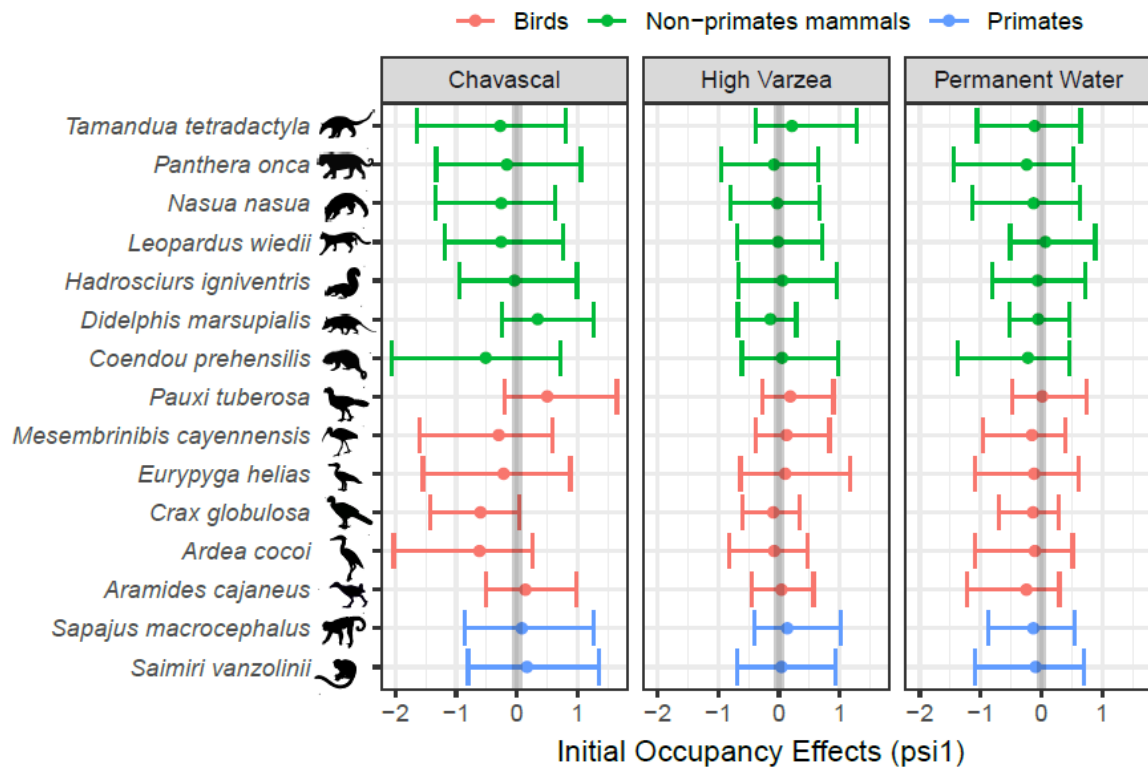
Model 2:  $\mu.\text{beta} \sim \text{dunif}(-20, 20)$ ;  $\text{sd}.\text{beta} \sim \text{dnorm}(0, 0.1)I(0,)$

Model 3:  $\mu.\text{beta} \sim \text{dnorm}(0, 0.001)$ ;  $\text{sd}.\text{beta} \sim \text{dnorm}(0, 0.001)I(0,)$

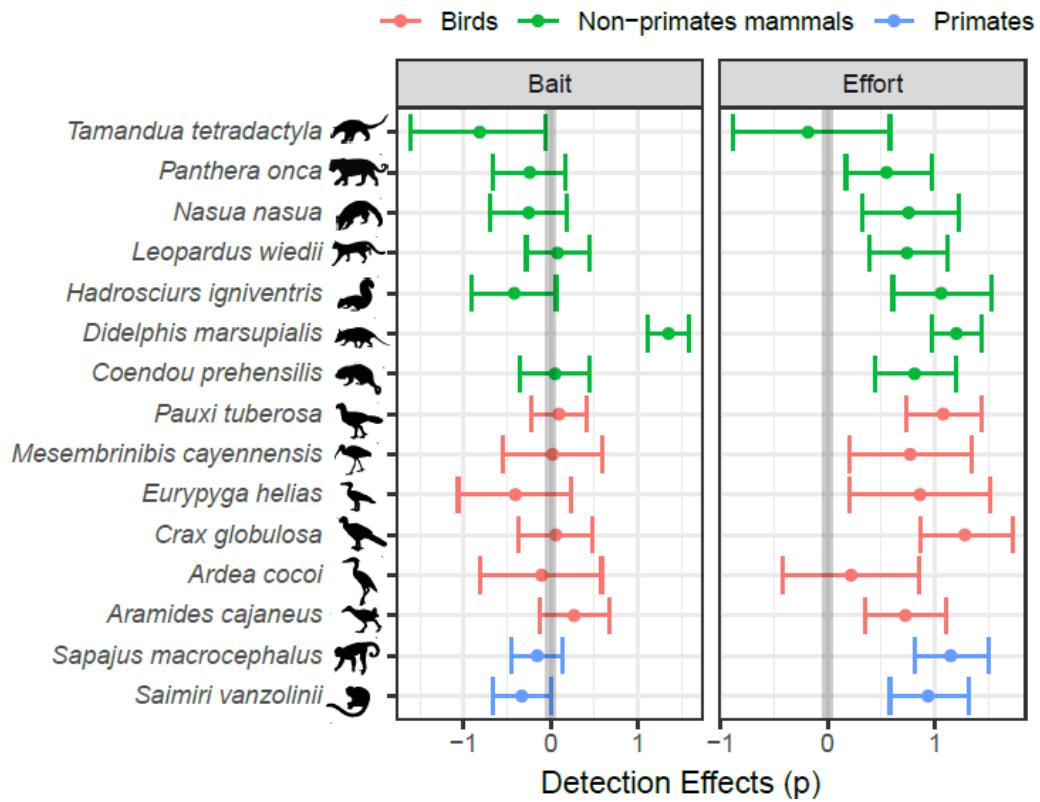
**Supporting Information 3** - Number of detections by species in the seven years of sampling in the Mamirauá SDR.



**Supporting Information 4** - Mean and 95% CRI of the effect of habitat classes on initial occupancy (psi1).



**Supporting Information 5** - Mean and 95% CRI of the effect of bait and effort on detection (p).



## **CHAPTER 2 - Modelling the impact of hunting on the coexistence of congeneric deer species in Central Amazonia**

Short title: Hunting and coexistence of *Mazama* species

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## **Abstract**

Long-term coexistence of sympatric species is dependent on segregation in at least one of three niche dimensions: space, time or feeding habits. Hunting by people can influence species' temporal and spatial patterns and consequently affect their coexistence. We tested the hypothesis that hunting influences spatial and temporal patterns of coexistence of two sympatric deer species (*Mazama americana* and *M. nemorivaga*) in central Amazonia. We described deer hunting patterns using data from an 18-year community-based hunting monitoring program, and predicted the spatial distribution of deer hunting trips. We used camera traps to (i) estimate the habitat use patterns of each species through conditional occupancy, (ii) evaluate whether these species interact, and (iii) assess how modelled hunting intensity affects deer habitat occupancy. We also tested the temporal overlap of activity time between both species and hunters. We did not find evidence of hunting effects on occupancy and interaction, nor of spatial segregation among the deer species. *M. americana* was primarily nocturnal and *M. nemorivaga* primarily diurnal. The overlap between species' temporal activities was relatively low, suggesting a temporal niche segregation between species. Hunting



activity was mainly diurnal and overlapped with *M. nemorivaga* active hours. However, we found that *M. americana* was more frequently hunted than *M. nemorivaga*. The probability of daytime activity was not influenced by hunting intensity. Temporal segregation, with asynchrony of activity periods, seems to be the mechanism behind the coexistence of *M. americana* and *M. nemorivaga* in Central Amazonia. The absence of hunting effects on brocket deer species in our study area suggest a low impact of harvest on both species' behavior. This indicates that contexts of low human density and large extensions of pristine forests can enable hunted brocket deer populations to be sustained through source-sink dynamics.

Keywords: conditional occupancy, ecological niche, habitat use, activity patterns, spatio-temporal patterns, hunting sustainability

## Introduction

Understanding the factors that allow the coexistence of species is of fundamental interest in ecology (Hart, Usinowicz & Levine, 2017). Long-term coexistence of species with similar niche is only possible through niche segregation and mechanisms that prevent competitive exclusion (Hardin, 1960; MacArthur & Levins, 1967). The three main dimensions of niche segregation are space (habitat use), time (activity patterns) and food (diet) (Schoener, 1974). Coexistence of competing species depends on the partial segregation in at least one dimension of their niche (Hardin, 1960; MacArthur & Levins, 1967). Therefore, as a result of long-term competition, adaptations in morphology and behavior of species are selected throughout their evolutionary history, and result in niche segregation that allows their coexistence (Rosenzweig, 1981; Leibold, 1998).

Spatial segregation can be understood as the partitioning of habitat use by potentially competing species, especially when food resources are limited (Price, 1978; Scott & Dunstone, 2000). Habitat use can vary across the geographic range of a species (Schaub *et al.*, 2011), being shaped by interspecific competition (Reif *et al.*, 2018) and coexistence of closely related species (Goldingay & Price, 1997). However, when the habitat use of two or more species overlap, temporal segregation may be more important to favor species coexistence (Schoener, 1974; Kronfeld-Schor & Dayan, 2003). Interspecific competition can strongly influence behavioral responses, typically resulting in asynchronous temporal activity patterns between competitor species (Di Bitetti *et al.*, 2008; Ferreguetti, Tomás & Bergallo, 2015).

Hunting by people can influence species' temporal and spatial patterns and consequently affect their coexistence (Gaynor *et al.*, 2018; Carricondo-Sanchez *et al.*, 2019). For instance, hunting of a given species may reduce its populations in areas with high hunting pressure and favor populations of less targeted competitors (Peres & Dolman, 2000; Di Bitetti *et al.*, 2008). In addition, an increase in the nocturnality of certain species has been observed in areas affected

by hunting (Di Bitetti *et al.*, 2008; Shamoan *et al.*, 2018). Even in areas subjected to numerically sustainable hunting, target species tend to change their behavior and interactions with other species (Ordiz, Bischof & Swenson, 2013; Lone *et al.*, 2015), potentially driving ecological cascading effects (Schmitz, Krivan & Ovadia, 2004).

The brocket deer (genus *Mazama*) are widely distributed in the Neotropics. The distribution of the red brocket deer (*M. americana*) and the brown brocket deer (*M. nemorivaga*) overlap virtually along the entire extent of the Amazon forest (Duarte & Vogliotti, 2016, Rossi & Duarte, 2016). Changes in population structure and activity patterns as a response to hunting pressure have been reported for both brocket deer species, but these changes are usually more significant for *M. americana* (Bodmer *et al.*, 1994; Peres, 1997). Harvest rates of *M. americana* are generally higher than those of *M. nemorivaga* (Bodmer & Lozano, 2001; Hurtado-Gonzales & Bodmer, 2004), mainly due to its higher yield in biomass (Jerozolimski & Peres, 2003). In addition, an increase in *M. americana*'s nocturnality has been detected in areas subjected to intense hunting (Di Bitetti *et al.*, 2008), even though the species is already primarily nocturnal, whereas *M. nemorivaga* is primarily diurnal (Oliveira *et al.*, 2016).

Previous studies in central Amazonia indicated that hunting, even when conducted for subsistence, may impact wild game populations, especially in areas closer to human settlements (Valsecchi, El Bizri & Figueira, 2014; Morcatty & Valsecchi, 2015). In addition, demand on wild meat in central Amazonia might have upscaled with the increase in human population in the last decades (IBGE, 2010). In this study we evaluate whether and how hunting intensity affects habitat use and activity patterns of coexistence of *M. americana* and *M. nemorivaga* in central Amazonia. First, we modeled hunting intensity across our study area and described the hunting patterns of both *Mazama* species. Then, using camera traps within a gradient of hunting intensity, we tested (1) if the two deer species segregate in at least one of the two tested niche dimensions (temporal or spatial); (2) whether the occupancy of *M. americana* decreases with

the increase in hunting intensity and favors the increase in the occupancy of *M. nemorivaga*; and (3) whether both species tend to be more nocturnal in areas with higher hunting intensity.

## Methods

### *Study area*

This study was conducted around the Amanã Lake within the Amanã Sustainable Development Reserve (ASDR; 01°S, 64°W; Fig. 1). This reserve is located between the Negro and Japurá rivers in the Central Amazon, covering an area of 23,500 km<sup>2</sup>, and is composed mainly by upland forest (*terra firme*) on *paleovárzea* soils (Irion *et al.*, 2010). The climate is equatorial (Af), according to the Köppen-Geiger classification, with an annual temperature of 22–36°C, a relative humidity of 80-100%, and an annual rainfall of 1500-3000 mm.

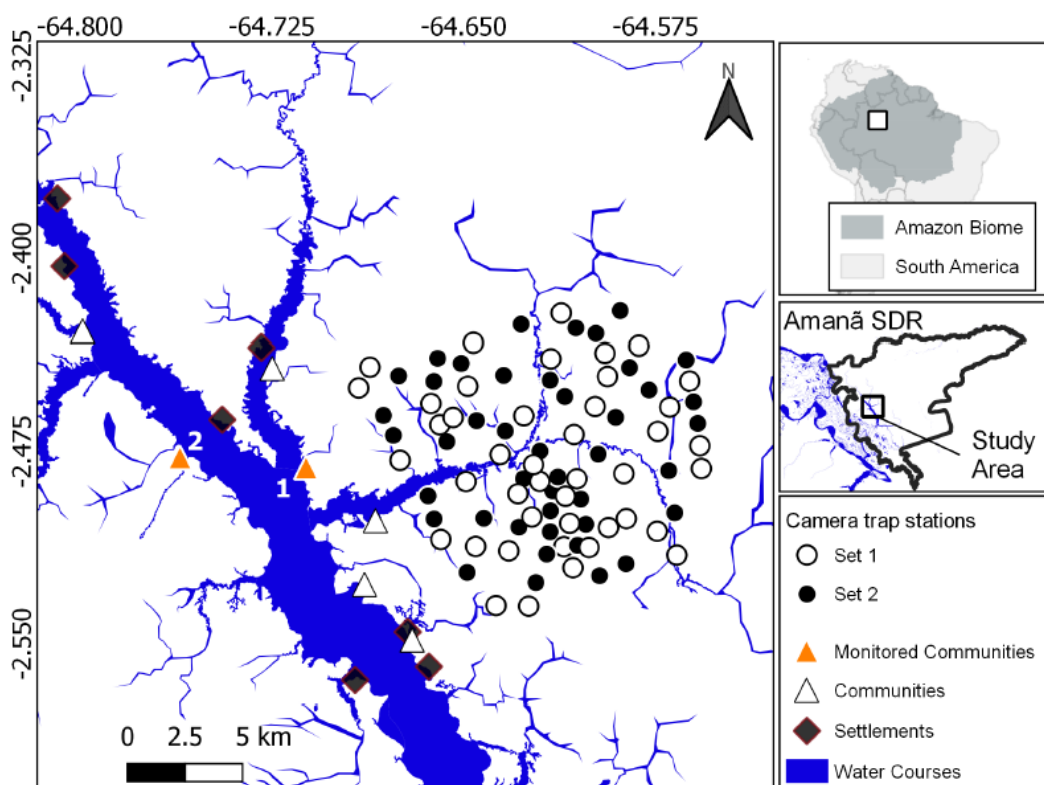


Figure 1 - Location of Amanã Sustainable Development Reserve, study area (inset), location of camera trap stations and communities monitored regarding *Mazama* spp. hunting.

ASDR is a 'sustainable use protected area' (Amazonas, 1998), which is a type of protected area where local people can live inside and are allowed to use natural resources within the boundaries of the protected area. There are nine human communities and 17 small settlements around Amanã Lake, with a population density of 0.39 people/km<sup>2</sup> (SIMDE/IDSM, 2018). These villages are isolated from the nearest urban center by approximately 100 km, 12 hours by regional boat, and their main source of food and income include small-scale agriculture, fishing, hunting and the extraction of other forest products (Peralta & Lima, 2019).

#### *Data collection*

*Deer hunting.* - Hunting data was collected in two communities participating in a long-term hunting monitoring system by the Mamirauá Institute (names of the communities were anonymized, and hereafter we refer to them as Community 1 and Community 2; Fig. 1). These two communities are composed of a total of 394 inhabitants residing in 84 households (SIMDE/IDSM, 2018). There are 66 declared hunters in these communities, and deer hunting is conducted mainly for local consumption (Valsecchi & Amaral, 2009). We obtained information through a participatory hunting monitoring system in operation for 18 years (2002 – 2019) in Community 1 and for 16 years (2002 – 2017) in Community 2. We hired one local research assistant within each community to record daily data on hunting trips provided voluntarily by hunters of the village onto a standardized form (Table S1). The form included the information of species killed, number of individuals killed, biomass (in kg) of each hunted specimen, time spent hunting, geographic location of the kill and whether the hunting trip was intentional or opportunistic, i.e. associated with other activities such as farming or fishing. We filtered and used for this study only hunting trips in which a deer specimen was killed. All

hunting localities were then visited and georeferenced using a handheld GPS. To ensure the quality and accuracy of the hunting data, completed forms were inspected monthly to detect any inaccuracy.

*Camera trap.* - We set up 86 camera trap stations across a gradient of distance from local communities, covering a total area of approximately 140 km<sup>2</sup> (Fig. 1). Each camera trap station was composed of two camera traps (model PC800 HyperFire®, ReconyxInc, Holmen, Wisconsin, USA) placed 4 m apart, facing each other, and 40 cm above the ground. Camera-traps were configured to take photographs 24 h per day and to record the date and time of each picture. Each time a camera-trap was triggered, a sequence of 10 pictures was taken, with one-second interval between photos. Data were collected from February to September 2017. Due to the limited number of equipment, we divided the 86 sampling stations into two sets of 43 stations each. The first set remained in operation for 63 days and, immediately after removing the camera traps of the first set, we established the second one, which remained in operation for up to 133 days. Camera trap station locations were alternated between the sampling sets, ensuring that the two sets had similar environmental conditions (Fig. 1; Table S2). The total sampling effort was 7,796 trap\*days. The average distance between adjacent stations was 986 m and varied from 507 to 1811 m.

#### *Data analysis*

*Deer hunting intensity and patterns.* - As we monitored only two local communities, we extrapolated the hunting intensity in the study area (within an approximately 2,300-km<sup>2</sup> region) using a Poisson point process model (*ppm*). We modelled the hunting points density according to two spatial covariates: (1) distance from hunting locations to the nearest water course, since rivers are the commuting route for community members; and (2) distance from hunting locations to the nearest community. The parameters of a *ppm* are estimated by maximum

likelihood. For this purpose, we used the function ‘Fit Point Process Model to Data (ppm)’ available in the package ‘spatstat’ (Baddeley, Rubak & Turner, 2015). We then used the fitted *ppm* to predict the density of deer hunts (hereafter 'hunting intensity') across the study area. Moreover, we used descriptive statistics to report the number of hunting trips per species and the percentage of intentional or opportunistic specimens hunted.

*Occupancy estimates.* – We used the estimated occupancy probability as a measure of habitat use. To match the sampling effort from the first set of camera-trap with the second one, as well as to avoid a potential bias caused by sampling duration on deer site occupancy estimates (see Steenweg *et al.*, 2018), we used only the first 63 days of sampling from the second set for occupancy estimates. Thus, the total sampling effort for the occupancy estimates was reduced to 5,111 trap\*days. We assembled a detection history matrix for *M. americana* and *M. nemorivaga*, defining a period of seven consecutive days as a sampling occasion. We computed Moran's I autocorrelation coefficient for each species based on the distance between stations that with at least one record and the rate of record per season (number of records / number of sampling occasions) using the package ‘ape’ (Paradis & Schliep, 2019) and we did not find spatial autocorrelation (*M. americana*: observed=0.03, expected=-0.02, sd=0.03, p.value=0.06; *M. nemorivaga*: observed=-0.09, expected=-0.05, sd=0.05, p.value=0.32). We analyzed the data using the ‘multispecies occupancy model for interacting species’ (Rota *et al.*, 2016). This model is a generalization of single-season occupancy models that can accommodate two or more interacting species and allows modeling the probability of two or more species to occupy the same location as a function of covariates.

To fit the models, we defined the occupancy ( $\Psi$ ) and detection ( $p$ ) covariates (Table 1). Hunting intensity and elevation were included in candidate models as a covariate for the probability of occupation of each species. Although we did not expect clear effects of elevation on species occupancy, we used this covariate in occupancy models to control for potential effects of the

variation in environmental requirements between the two species. Despite its low variation in our study area, elevation is usually associated with changes in vegetation structure and plant species composition in the Amazon (Junk, Bayley & Sparks, 1989; Wittmann & Junk, 2003). Hunting intensity was also included in candidate models as a covariate for the probability of species co-occurrence at each site. The covariate 'effort' (number of days that each camera trap station was active within occasions) was maintained in all models. We built 18 competing models considering the influence of covariates on species in models with or without second-order interactions (see all models in Table S3). We used the Akaike Information Criterion adjusted for small sample size (AICc) to classify competing models (Burnham & Anderson, 2002) and conducted an assessment of the model's fit for the global model using the parametric initialization method (Fiske & Chandler, 2011). We considered that models with  $\Delta\text{AICc} < 2$  had similar support (Burnham & Anderson, 2002). We also estimated the overall probability of occupancy for each species using the *predict* function of the package *unmarked* with  $10^5$  simulations weighted by the best ranked model (Fiske & Chandler, 2011). All analyses were conducted in R (R Core Team, 2021) with the package 'unmarked' (Fiske & Chandler, 2011).



Table 1 - Covariates used to build occupancy models for *M. americana* and *M. nemorivaga* at study area.

<b>Code</b>	<b>Description</b>	<b>Range of values</b>	<b>Fitted Parameters</b>
hunt	Number of hunted individuals per km <sup>2</sup> (see Deer hunting patterns)	0 - 0.23 individuals/km <sup>2</sup>	Occupancy of each species; Interaction between species
elevation	Elevation in relation to sea level (digital terrain model)	38 - 45 m.a.s.l.	Occupancy of each species
effort	Number of days for each sampling occasion	1 - 7 days	Detection of each species
trail	Location of camera trap in relation to a human trail	0 - off trail / 1 - on trail	Detection of each species

*Activity pattern.* - For the activity pattern analysis, we used the entire dataset (7,796 trap\*days) and considered that photographs obtained <30 min apart did not constitute independent records. To calculate the activity pattern of hunters, we pooled all data of hunting trips from the hunting monitoring period and calculated the frequency of hunting trips that fell within each 24-hour of the day. To do so, we added the traveled time – calculated using the total distance traveled by hunters in each hunting trip recorded and considering boat speed of 10km/h – to the departure time from the community and subtracted the travel time from the arrival time back at the community. This correction was performed considering that hunters usually use water courses to commute to hunting areas, start actively hunting only when they arrive at the hunting location, and stop hunting when departing from hunting regions.

To compare the activity patterns between deer species and between deer and hunters, we compared the daily activity patterns among them. We used the ‘activity’ package to fit a flexible circular kernel distribution to time-of-detection data (Rowcliffe, 2019). To assess overlapping activity patterns between deer species and between each species and hunters, we estimated a coefficient of overlap using the ‘overlap’ package (Ridout & Linkie, 2009). This package calculates three estimates of activity pattern overlap based on times of observations for two species (Dhat1, Dhat4 and Dhat5). Coefficients range from 0 to 1, where 0 indicates completely distinct activity patterns, and 1 represents identical patterns (Ridout & Linkie, 2009). The dhat4 estimator was used in this study as this is the recommended one when both samples are larger than 50. We performed Watson's test for homogeneity on two samples of circular data to determine whether daily activity patterns were significantly different (Agostinelli & Lund, 2017).

In addition, we assessed the effects of hunting intensity on the probability of daytime activity of the species. For this we evaluate the proportion of daytime records (06:00 - 17:59) as a function of the estimated hunting intensity for each camera trap station with at least one record. We fitted a generalized linear model (GLM) with binomial distribution for proportional data for each species (R Core Team, 2021).

## **Results**

*Deer hunting intensity and patterns.* - During the monitored period, 159 hunting trips of *Mazama* spp. were recorded, with 133 individuals of *M. americana* harvested, a total biomass of 3900.5 kg, and 26 individuals of *M. nemorivaga* harvested, a total biomass of 350 kg. Deer hunting intensity showed a strong relationship with the distance to nearest water courses and local communities. For both variables, we observed an increase in the estimated hunting

intensity at shorter distances (Distance from water course:  $Z=-6.93$ ,  $p<0.001$ ; Distance from communities:  $Z=-7.25$ ,  $p<0.001$ ; Fig. 2). Hunters used 35 localities to hunt deer, spreading up to 15 km away from the hunters' villages. However, 70% of hunting trips occurred within a 5-km distance from the villages. Hunters killed most of the deer individuals during the day ( $n = 111$ ; 69.8%), and declared to intentionally hunt *M. americana* in 31.7% of the trips, while *M. nemorivaga* was hunted intentionally in 34.8% of the trips (see complete data in Table S4).

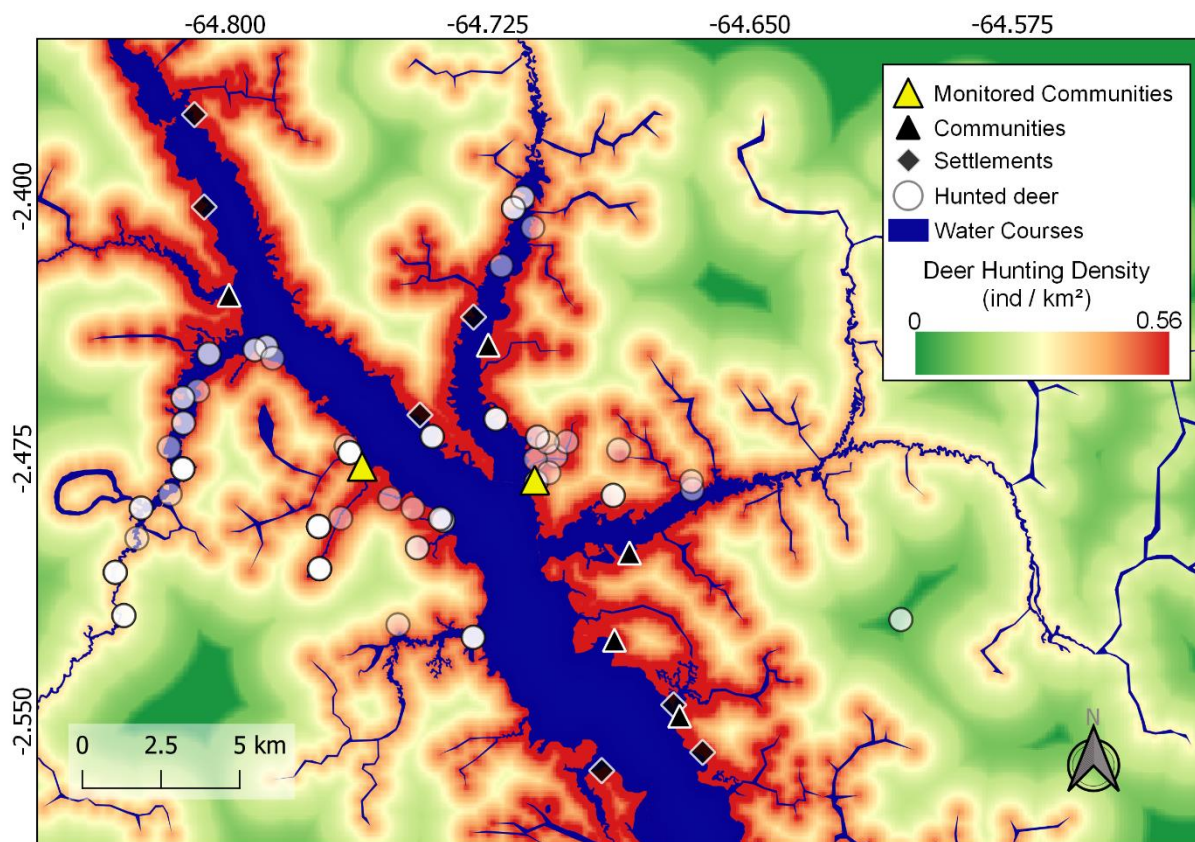


Figure 2 - Predicted deer hunting intensity between 2012-2019 in the study area using a Poisson point process model. Transparency circles indicates deer harvest locations and circles with greater opacity indicates overlapping points.

*Occupancy estimates.* - We recorded *M. americana* on 83 sampling occasions at 47 camera trap stations, and *M. nemorivaga* on 35 sampling occasions at 22 camera trap stations. Model ranking indicated that the selected covariates did not affect site occupancy by the species or the interaction between species (Table 2). Of the 18 candidate models tested (Table S3), three had  $\Delta\text{AICc} < 2$ , all including a null effect on occupancy.

Table 2 - Top ranked models for occupancy modeling of *M. americana* and *M. nemorivaga* at the Amanã Sustainable Development Reserve.

<b>Modnames</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta\text{AICc}</math></b>	<b>AICcWt</b>	<b>Cum.Wt</b>
psi(.)p(effort)	6	791.109	0	0.309	0.309
psi(.)p(effort+trail)	8	791.968	0.860	0.200	0.510
psi(. ~interaction)p(effort)	7	792.561	1.453	0.149	0.659

The predicted occupancy based on the best ranked model was higher for *M. americana* (0.70 - 95% CI, 0.52 to 0.83) than for *M. nemorivaga* (0.37 - 95% CI, 0.22 to 0.54). The ranking of models did not indicate effects of the interaction between occupancies of both species. Moreover, the most likely state of occupancy of sites indicates that species do not tend to aggregate or avoid one another (Fig. 3).

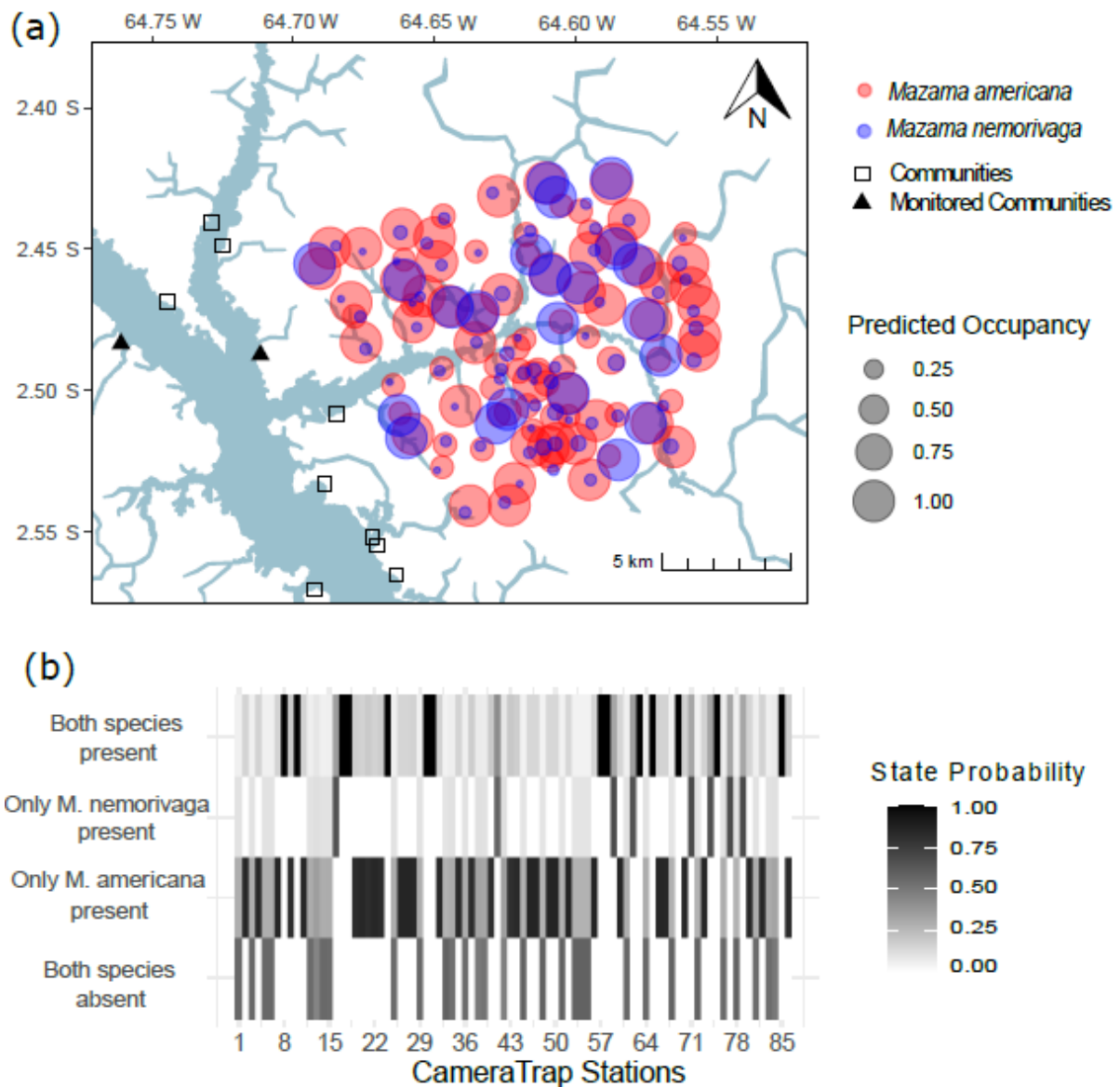


Figure 3 - (a) Predicted occupancy of each species in the sampled area and (b) probability of each occupation state at each camera trap station.

*Activity pattern.* - In total, we obtained 149 independent records of *M. americana* (in 57 camera trap stations) and 58 of *M. nemorivaga* (in 25 camera trap stations). The activity pattern was significantly different between species ( $T=1.69$ ,  $p<0.001$ ), with an overlap of 0.42 (Dhat4). Brown brocket deer showed higher activity during the day, while red brocket deer showed higher activity at night. The overlap between hunters' activity period with the activity period

of *M. nemorivaga* (Dhat4=0.80, T=0.20,  $p<0.05$ ) was greater than with the activity period of *M. americana* (Dhat4=0.58, T=2.37,  $p<0.001$ , Fig. 4). The difference in the activity patterns between *M. nemorivaga* and hunters was due to the almost zero activity of the species between 21:00 and 4:00. We found no influence of hunting intensity on the probability of daytime activity by any brocket deer species (Table 3).

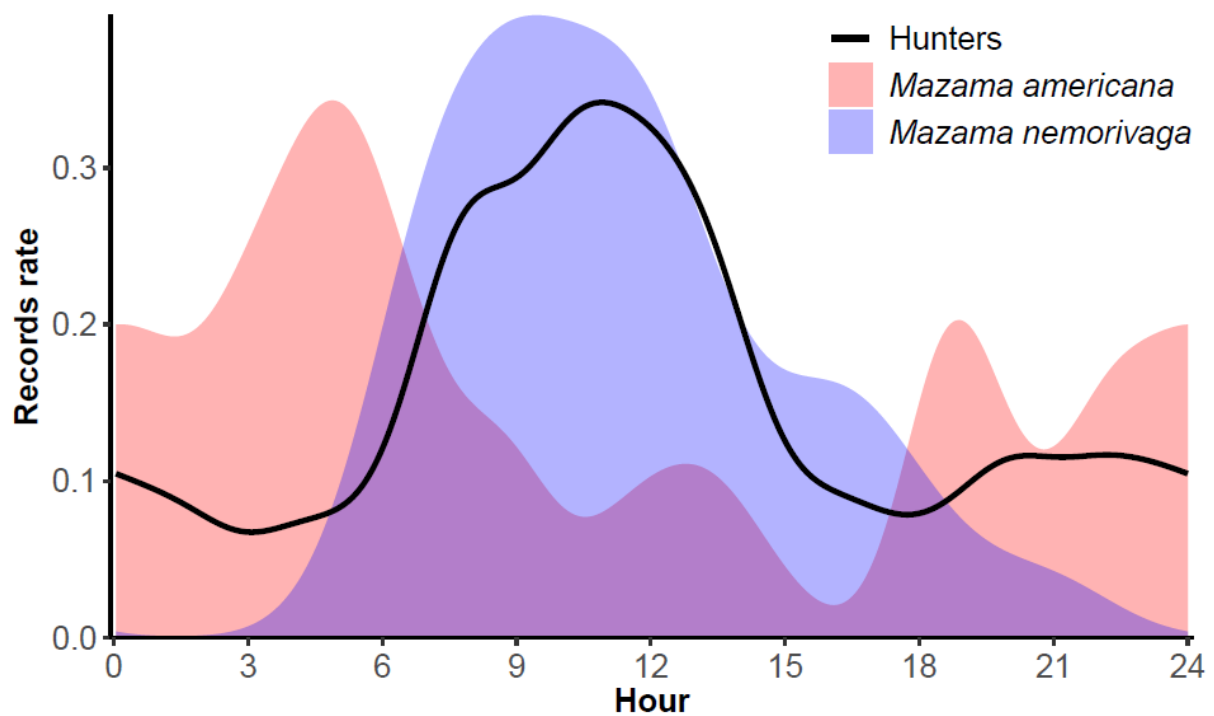


Figure 4 – Activity patterns of *Mazama americana*, *M. nemorivaga* and hunters in the study area.

Table 3 – Estimates of generalized linear models assessing the influence of hunting on the probability of daytime activity of *Mazama americana* and *Mazama nemorivaga*. Lower and upper values of confidence intervals (CI) and p-value of parameters are also presented.

	<i>Mazama americana</i>				<i>Mazama nemorivaga</i>			
	Estimate	Lower CI	Upper CI	p	Estimate	Lower CI	Upper CI	p
Intercept	-0.916	-1.29	-0.56	<0.001	3.477	1.97	7.17	0.004
Hunting intensity	-0.106	-0.59	0.32	0.645	1.98	-0.09	6.71	0.234
Observations	57				25			
R <sup>2</sup>	0.001				0.033			

## Discussion

We found no evidence of a hunting effect on the occupancy and interaction between *M. americana* and *M. nemorivaga*. Although the camera stations covered most of the estimated hunting intensity gradient, the closest camera trap station was installed more than 2.5 km away from a human community. Thus, we acknowledge that most of the camera trap stations were far away from areas of higher hunting intensity. In addition, 80% of stations were placed more than 5 km away from villages, and more than 70% of deer hunting events were recorded near the villages (<5 km). In fact, the estimated hunting intensity in the area sampled by the camera trap grid was less than half of the estimated intensity closest to human communities. Therefore, we recognize that this limitation in our sampling design may have affected our findings. On the other hand, the sampled area is located in a region characterized by low human density and with large extensions of continuous primary forest, enabling wild animal populations to be sustained through source-sink dynamics (Novaro, Redford & Bodmer, 2000; Antunes *et al.*, 2016). Therefore, we suggest that the forests in our sampled region can function as a source for *Mazama* spp., at least at distances greater than 2.5 km from human communities.

Assuming that more abundant species tend to have higher site occupancy (Gaston *et al.*, 2000), the high site occupancy of *M. americana* suggests it has higher abundance than *M. nemorivaga* in the study area. Similar findings were found in the Peruvian Amazon, where the density of *M. americana* was twice as large as that of *M. nemorivaga* (Salovaara *et al.*, 2003). The difference in occupancy observed in our study, however, does not indicate that *M. americana* occupancy influences *M. nemorivaga*'s. In fact, we did not detect spatial segregation between the two congeneric deer, although spatial segregation patterns between congeneric species seems to be common (Reagan, 1992; Chesson, 2000; Winchell *et al.*, 2018). Considering that spatial segregation is more common when food resources are limited (Schoener, 1974; Scott & Dunstone, 2000), it is possible that the high primary productivity of *paleovárzea* forests (Irion *et al.*, 2010) results in sufficient amounts of food resources for both *Mazama* species, and allows an overlap of niche in the spatial dimension in our study area. The variation in vegetation structure as a result of the elevation did not influence the occupancy of any of the species. Besides, it is important to highlight that the period in which the camera trap sampling occurred coincides with the period of greatest fruit availability (Haugaasen & Peres, 2005), and seasonal changes in habitat use might be expected in periods of fruit scarcity.

Given that our analysis does not indicate spatial segregation between brown and red brocket deer and that their diet is very similar (Bodmer 1991, Bodmer & Ward 2006, Rossi *et al.*, 2010), the observed asynchrony of activity periods may be the mechanism creating conditions for the two species to spatially coexist. Temporal avoidance is common for closely related species (Kronfeld-Schor & Dayan, 2003, Nagy-Reis *et al.*, 2019; Rasphone, Kamler & Macdonald, 2020). The primarily nocturnal pattern of activity of *M. americana* and diurnal of *M. nemorivaga* agrees with the patterns observed in other studies and seem to be related to the phylogenetic restrictions of the species (Oliveira *et al.*, 2016). The dense vegetation cover in our study area allows *M. nemorivaga* activity even in the hottest periods of the day, contrary



to what occurs with *M. gouazoubira*, from the same evolutionary lineage, in areas with greater exposure to solar radiation (Oliveira *et al.*, 2016).

Current hunting pressure by humans does not seem to be responsible for this temporal segregation pattern, as we have not observed differences in the activity patterns according to estimated hunting density in the area sampled by camera traps. Other studies indicated a prevalence of nocturnal activity of *M. americana* in the Amazon (Rivero, Rumiz & Taber, 2005; Tobler, Carrillo-Percestequi & Powell, 2009) and in other biomes (Di Bitetti *et al.*, 2008; Ferregueti *et al.*, 2015). In fact, *Mazama* species that are phylogenetically close show similar activity patterns: while *M. nemorivaga* and *M. gouazoubira* tends to be more diurnal, *M. americana*, *M. nana* and *M. bororo* tends to be more nocturnal (Oliveira *et al.*, 2016). Although not tested here, we cannot reject the hypothesis that competition with other large-sized ungulate species, such as collared peccary (*Pecari tajacu*), white-lipped peccary (*Tayassu pecari*) and tapirs (*Tapirus terrestris*), and the presence of predators, such as puma (*Puma concolor*) and jaguar (*Panthera onca*), may influence the current behavior and evolutionary history of *Mazama* species.

Even with hunting times overlapping more with *M. nemorivaga* activity times, we found that *M. americana* was more frequently hunted in our study area. In addition to the apparent greater abundance of *M. americana*, hunters' preferences may also play a role in determining higher hunting frequency for this species. Some reports from hunters indicate that a taboo concerning the palatability of brown brocket deer meat is culturally shared among villagers of our study area. Other studies in the Amazon indicated that palatability was a determinant for greater preference for *M. americana* over *M. nemorivaga* by hunters (Ramos *et al.*, 2020). In fact, palatability seems to be an important factor in hunters' prey choice decisions (Koster *et al.*, 2010). Previous studies conducted in our study site revealed that brown brocket deer occupy the 18th position among 41 game species locally consumed in terms of meat flavor, while the

red brocket deer occupies the 9th position (L. P. Lemos *et al.*, unpublished data). Moreover, hunters can favor red brocket deer hunting due to its higher yield in biomass, since its mean body mass is almost two-fold greater than that of brown brocket deer (Robinson & Redford, 1986; Jerozolimski & Peres, 2003).

Our results suggest that the cumulative hunting pressure over our studied period may not have been high enough to affect species' occupancy, distribution and activity patterns in our sampled area. Hunting was not retained as a covariate in the most plausible models for occupancy. In addition, we did not detect behavioral shifts determined by hunting in areas closer to the villages, as previously detected for *M. americana* in the southern portion of its distribution (Di Bitetti *et al.*, 2008). The lower level of hunting pressure for both species of deer is evidenced by the larger proportion of opportunistic deer hunting trips compared to intentional trips. Additionally, rodents and other large ungulates, such as tapir and peccaries, are usually dominant over deer in hunting profiles in other Amazonian sites (Stafford, Preziosi & Sellers, 2017), so we can assume that deer do not comprise the bulk of preferred and more frequently targeted game in our study area.

Other evidence revealed here supports the claim that deer hunting is likely to be a low-impacting activity in our study area. One could assume that if hunting is concentrated in locations near to the villages, the maintenance of harvests near settlements over time could be interpreted as a proxy of game availability. We have shown that the majority of deer hunting trips occur in a core area of up to 5 km far from the villages. This core catchment area is smaller than the mean distances registered for harvests of *Mazama* spp. in northern Amazon (see Richard-Hansen *et al.*, 2019) and similar to catchment areas of Indigenous villages in the western Amazon (see Ohl-Schacherer *et al.*, 2007). Additionally, considering deer reproductive traits, Novaro *et al.* (2000) suggested that at least 52% and 47% of the area used for hunting *M. americana* and *M. nemorivaga*, respectively, need to remain un hunted to ensure population

dispersion and recovery through source-sink dynamics. The Protected Area management plan allows hunters to use up to 40% of the landscape in our study site, leaving the remaining 60% un hunted to act as source areas (Amazonas, 2020).

In this study, we showed that *M. americana* and *M. nemorivaga* overlap in the spatial dimension and segregate in the temporal dimension of the niche. *M. americana* is more frequently hunted than *M. nemorivaga*, possibly because of the higher preference by the hunters of the former deer species. Furthermore, our data suggest that hunting pressure at distances greater than 2.5 km away from human communities does not appear to be affecting deer occupancy nor activity patterns in our study region. We highlight that the forests in our study area are quite pristine, since habitats converted for swidden cultivation and human habitation represent a very small proportion of the habitat available for wild fauna, favoring the source-sink dynamics. Our study is an example of how long-term monitoring of hunting can be allied to ecological surveys on tropical species to shed light on the factors affecting the coexistence of sympatric species. By adopting this integrative approach, our findings provide relevant information to the development of management actions and conservation measures for these species.

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### Supplementary data

Table S1 - Survey datasheet of hunting monitoring.

Community: \_\_\_\_\_

Name of collector: \_\_\_\_\_ Number of hunters: \_\_\_\_\_

Date when hunting started: \_\_/\_\_/\_\_ and finished: \_\_/\_\_/\_\_ Time of departure from the village: \_\_:\_\_ Time of arrival at the village: \_\_:\_\_

Individual Id	Species (Local name)	Biomass (Kg)*	Instruments applied	Location of the kill (Local name)	Period of the day (day/night)	Hunting was intentional or opportunistic?	If opportunistic, what were you doing when you targeted the animal?
1							
2							
3							
4							
5							
6							
7							
8							
9							
10							
11							
12							
13							
14							
15							

Table S2 - Means and 95% credible interval of environmental and anthropogenic variables in the first and in the second set of camera trap sampling

	<b>Set 1</b>	<b>Set 2</b>
Distance from human communities (m)	8515 (3861-14285)	8588 (3654-14560)
Distance from water course (m)	932 (132-2398)	840 (106-1935)
Elevation (m. a. s. l)	41.7 (39.6-43.8)	41.8 (38.9-44.3)
Deer hunting intensity (individuals/km <sup>2</sup> )	0.043 (0.001-0.161)	0.042 (0.002-0.134)

Table S3 - Ranking of all models for occupancy modeling of *Mazama americana* and *M. nemorivaga* at Amanã Sustainable Development Reserve. Standard error (SE) values in parentheses.

Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt	psi([ <sup>^</sup> M. americana`] (Intercept))	psi([ <sup>^</sup> M. americana`] elev)	psi([ <sup>^</sup> M. americana`] hunt)	psi([ <sup>^</sup> M. nemorivaga`] (Intercept))	psi([ <sup>^</sup> M. nemorivaga`] elev)	psi([ <sup>^</sup> M. nemorivaga`] hunt)	psi([ <sup>^</sup> M. americana``: nemorivaga`] (Intercept))	psi([ <sup>^</sup> M. americana``: nemorivaga`] hunt)	p([M. americana] (Intercept))	p([M. americana] effort)	p([M. americana] Trail)	p([M. nemorivaga] (Intercept))	p([M. nemorivaga] effort)	p([M. nemorivaga] Trail)
psi(.)p(effort)	6	791.109	0	1	0.309	-389.023	0.309	0.86 (0.39)	-	-	-0.53 (0.36)	-	-	-	-	-4.1 (1.52)	0.35 (0.22)	-	-5.32 (2.89)	0.49 (0.42)	-
psi(.)p(effort+trail)	8	791.968	0.86	0.651	0.201	-387.049	0.51	0.97 (0.43)	-	-	-0.44 (0.37)	-	-	-	-	-4.07 (1.51)	0.35 (0.22)	-0.68 (0.55)	-5.31 (2.88)	0.5 (0.41)	-1.59 (1.11)
psi(. ~int)p(effort)	7	792.561	1.453	0.484	0.149	-388.563	0.659	0.56 (0.46)	-	-	-1.2 (0.88)	-	-	0.91 (1.06)	-	-4.11 (1.53)	0.36 (0.22)	-	-5.31 (2.89)	0.49 (0.42)	-
psi(. ~int)p(effort+trail)	9	794.087	2.978	0.226	0.07	-386.859	0.729	0.75 (0.52)	-	-	-0.89 (0.87)	-	-	0.61 (1.04)	-	-4.06 (1.51)	0.35 (0.22)	-0.66 (0.56)	-5.3 (2.88)	0.49 (0.41)	-1.56 (1.12)
psi(. ~int(hunt))p(effort)	8	794.969	3.861	0.145	0.045	-388.55	0.773	0.56 (0.46)	-	-	-1.2 (0.88)	-	-	0.91 (1.06)	-0.05 (0.31)	-4.1 (1.52)	0.35 (0.22)	-	-5.3 (2.88)	0.49 (0.41)	-
psi(elevation)p(effort)	8	795.044	3.935	0.14	0.043	-388.587	0.817	0.86 (0.4)	-0.1 (0.34)	-	-0.54 (0.36)	0.26 (0.3)	-	-	-	-4.1 (1.52)	0.35 (0.22)	-	-5.3 (2.87)	0.49 (0.41)	-
psi(hunt)p(effort)	8	795.159	4.051	0.132	0.041	-388.644	0.857	0.87 (0.4)	-	-0.26 (0.3)	-0.53 (0.36)	-	0.01 (0.3)	-	-	-4.11 (1.52)	0.35 (0.22)	-	-5.31 (2.88)	0.49 (0.41)	-
psi(hunt)p(effort+trail)	10	796.047	4.938	0.085	0.026	-386.557	0.884	1 (0.45)	-	-0.31 (0.31)	-0.44 (0.37)	-	-0.04 (0.3)	-	-	-4.09 (1.51)	0.35 (0.22)	-0.71 (0.55)	-5.31 (2.88)	0.5 (0.41)	-1.6 (1.11)
psi(elevation)p(effort+trail)	10	796.189	5.08	0.079	0.024	-386.628	0.908	0.99 (0.44)	-0.15 (0.37)	-	-0.45 (0.37)	0.24 (0.3)	-	-	-	-4.07 (1.51)	0.35 (0.22)	-0.7 (0.55)	-5.3 (2.87)	0.49 (0.41)	-1.56 (1.12)
psi(. ~int(hunt))p(effort+trail)	10	796.556	5.447	0.066	0.02	-386.811	0.928	0.74 (0.52)	-	-	-0.89 (0.87)	-	-	0.62 (1.04)	-0.1 (0.32)	-4.06 (1.51)	0.35 (0.22)	-0.66 (0.56)	-5.3 (2.88)	0.49 (0.41)	-1.57 (1.12)
psi(elevation ~int)p(effort)	9	796.573	5.465	0.065	0.02	-388.102	0.948	0.55 (0.47)	-0.16 (0.36)	-	-1.24 (0.9)	0.28 (0.31)	-	-	-	-4.1 (1.52)	0.35 (0.22)	-	-5.29 (2.87)	0.49 (0.41)	-
psi(hunt ~int)p(effort)	9	796.699	5.59	0.061	0.019	-388.165	0.967	0.57 (0.47)	-	-0.27 (0.3)	-1.23 (0.91)	-	0.06 (0.32)	0.95 (1.09)	-	-4.11 (1.52)	0.35 (0.22)	-	-5.3 (2.89)	0.49 (0.41)	-
psi(hunt ~int)p(effort+trail)	11	798.295	7.186	0.028	0.008	-386.364	0.976	0.78 (0.54)	-	-0.31 (0.31)	-0.91 (0.9)	-	0 (0.31)	0.62 (1.07)	-	-4.08 (1.51)	0.35 (0.22)	-0.7 (0.55)	-5.31 (2.88)	0.5 (0.41)	-1.57 (1.12)
psi(elevation ~int)p(effort+trail)	11	798.381	7.273	0.026	0.008	-386.407	0.984	0.75 (0.53)	-0.2 (0.39)	-	-0.96 (0.9)	0.26 (0.31)	-	0.67 (1.07)	-	-4.07 (1.51)	0.35 (0.22)	-0.68 (0.56)	-5.29 (2.87)	0.49 (0.41)	-1.53 (1.12)
psi(hunt ~int(hunt))p(effort)	10	799.031	7.923	0.019	0.006	-388.049	0.99	0.59 (0.49)	-	-0.41 (0.43)	-1.16 (0.9)	-	-0.19 (0.64)	0.89 (1.08)	0.38 (0.82)	-4.11 (1.52)	0.35 (0.22)	-	-5.31 (2.89)	0.49 (0.42)	-
psi(elevation ~int(hunt))p(effort)	10	799.12	8.011	0.018	0.006	-388.093	0.995	0.55 (0.47)	-0.16 (0.36)	-	-1.23 (0.9)	0.28 (0.31)	-	0.95 (1.08)	-0.04 (0.31)	-4.09 (1.52)	0.35 (0.22)	-	-5.29 (2.87)	0.49 (0.41)	-
psi(hunt ~int(hunt))p(effort+trail)	12	800.658	9.55	0.008	0.003	-386.192	0.998	0.84 (0.59)	-	-0.49 (0.46)	-0.8 (0.91)	-	-0.31 (0.64)	0.51 (1.08)	0.46 (0.82)	-4.09 (1.51)	0.35 (0.22)	-0.71 (0.55)	-5.32 (2.88)	0.5 (0.41)	-1.57 (1.12)
psi(elevation ~int(hunt))p(effort+trail)	12	801.006	9.897	0.007	0.002	-386.366	1	0.74 (0.53)	-0.2 (0.39)	-	-0.95 (0.9)	0.26 (0.31)	-	0.68 (1.07)	-0.09 (0.31)	-4.07 (1.51)	0.35 (0.22)	-0.68 (0.56)	-5.29 (2.87)	0.49 (0.41)	-1.55 (1.12)



Table S4 - Hunting records of *Mazama americana* and *M. nemorivaga* in the Amanã Sustainable Development Reserve between 2002 to 2019

Period of the day	Hunting strategy	Instrument											Total Overall	
		<i>Mazama americana</i>					<i>Mazama nemorivaga</i>							
		Firearm	Firearm and dogs	Firearm and a machete	Bludgeon	No info.	Total	Firearm	Firearm and dogs	Firearm and a machete	Bludgeon	No info.		Total
<b>Day</b>	<b>Intentional hunts</b>													
	Active search on hunting trail	1	3	-	-	-	4	3	1	-	-	-	4	8
	Hunting on board of canoe	-	-	-	-	-	-	-	-	-	-	-	-	0
	Active search in the forest	3	-	-	-	-	3	1	-	-	-	-	1	4
	Hunting by the river banks	1	-	-	-	-	1	-	-	-	-	-	-	1
	Active search	11	6	-	-	-	17	2	1	1	-	-	4	21
	<b>Total intentional</b>	<b>16</b>	<b>9</b>	<b>-</b>	<b>-</b>	<b>-</b>	<b>25</b>	<b>6</b>	<b>2</b>	<b>1</b>	<b>-</b>	<b>-</b>	<b>9</b>	<b>34</b>
	<b>Opportunistic hunts</b>													
	On agricultural fields	2	-	-	-	-	2	-	-	-	-	-	-	2
	On islands during high river water levels	21	-	-	-	-	21	3	-	-	-	-	3	24
	While spotlighting other game	1	-	-	-	-	1	-	-	-	-	-	-	1
	On the way to agricultural fields	8	-	-	-	-	8	5	-	-	-	-	5	13
	While fishing	1	-	-	-	-	1	1	-	-	-	-	1	2
	While extracting other forest products	18	3	2	1	-	24	3	-	-	1	-	4	28
	<b>Total opportunistic</b>	<b>51</b>	<b>3</b>	<b>2</b>	<b>1</b>	<b>-</b>	<b>57</b>	<b>12</b>	<b>-</b>	<b>-</b>	<b>1</b>	<b>-</b>	<b>13</b>	<b>70</b>
	No info.	3	1	-	-	2	6	1	-	-	-	-	1	7
	<b>Total during the day</b>	<b>70</b>	<b>13</b>	<b>2</b>	<b>1</b>	<b>2</b>	<b>88</b>	<b>19</b>	<b>2</b>	<b>1</b>	<b>1</b>	<b>-</b>	<b>23</b>	<b>111</b>
<b>Night</b>	<b>Intentional</b>													
	Active search on hunting trail	1	-	-	-	-	1	-	-	-	-	-	-	1
	Hunting on board of canoe	9	-	2	-	-	11	1	-	-	-	-	-	11
	Active search in the forest	-	-	-	-	-	-	-	-	-	-	-	-	0
	Hunting by the river banks	-	-	-	-	-	-	-	-	-	-	-	-	0
	Active search	1	1	-	-	-	2	-	-	-	-	-	-	2
	<b>Total intentional</b>	<b>11</b>	<b>1</b>	<b>2</b>	<b>-</b>	<b>-</b>	<b>14</b>	<b>1</b>	<b>-</b>	<b>-</b>	<b>-</b>	<b>-</b>	<b>1</b>	<b>15</b>
	<b>Opportunistic</b>													
	On the agricultural fields	2	-	-	-	-	2	-	-	-	-	-	-	2
	On islands during high river water levels	1	-	-	-	-	1	-	-	-	-	-	-	1
	While spotlighting other game	17	-	-	-	-	17	-	-	-	-	-	-	17
	On the way to agricultural areas	1	-	-	-	-	1	-	-	-	-	-	-	1
	While fishing	-	-	-	-	-	-	-	-	-	-	-	-	0
	While extracting other forest products	6	-	1	-	-	7	-	-	-	-	-	-	7
	<b>Total opportunistic</b>	<b>27</b>	<b>-</b>	<b>1</b>	<b>-</b>	<b>-</b>	<b>28</b>	<b>-</b>	<b>-</b>	<b>-</b>	<b>-</b>	<b>-</b>	<b>-</b>	<b>28</b>
	No info.	2	-	-	-	-	2	-	-	-	-	-	-	2
	<b>night</b>	<b>40</b>	<b>1</b>	<b>3</b>	<b>-</b>	<b>-</b>	<b>44</b>	<b>1</b>	<b>-</b>	<b>-</b>	<b>-</b>	<b>-</b>	<b>1</b>	<b>45</b>
	No info. Overall					1	1	-	-	-	-	-	2	3
	<b>Total Overall</b>						<b>133</b>	<b>2</b>	<b>2</b>	<b>1</b>	<b>1</b>	<b>-</b>	<b>26</b>	<b>159</b>

## CONCLUSÃO

Nosso estudo fez uso de um amplo conjunto de dados de armadilhas fotográficas e monitoramentos de longo prazo da caça e do ciclo hidrológico na Amazônia Central. Com a adoção dessa abordagem integrativa, nossos achados fornecem informações relevantes sobre o status e dinâmica da fauna em áreas de uso sustentável. Estas informações são fundamentais para subsidiar as estratégias de conservação de espécies e uso sustentável dos recursos naturais pelas populações tradicionais.

No primeiro capítulo revelamos que a probabilidade de colonização ou de extinção de nenhuma espécie foi influenciada pela intensidade da inundação. De forma similar, a riqueza de espécies se manteve estável e a diversidade apresentou baixa variação ao longo dos anos. Reforçamos a indicação de que a composição da fauna de aves de solo e mamíferos na RDSM é determinada pelo filtro ambiental imposto pelos pulsos de inundação, limitando a ocorrência de espécies que não tem capacidade de passar prolongados períodos sem o estrato terrestre disponível. A seleção de populações altamente adaptadas associada à menor intensidade dos pulsos de inundação em relação à Amazônia Ocidental parece ainda limitar os impactos das variações da intensidade das cheias sobre estas espécies na RDSM.

No segundo capítulo mostramos que *Mazama americana* e *M. nemorivaga* se sobrepõem na dimensão espacial e segregam na dimensão temporal do nicho. *M. americana* é caçado com mais frequência do que *M. nemorivaga*, possivelmente devido à preferência dos caçadores. Além disso, nossos dados sugerem que a pressão de caça a distâncias maiores que 2,5 km das comunidades humanas não parece estar afetando a ocupação nem os padrões de atividade dos cervos em nossa região de estudo. Destacamos que as florestas em nossa área de estudo são bastante preservadas, uma vez que os habitats convertidos para agricultura e habitação humana

representam uma proporção muito pequena do habitat disponível para a fauna silvestre, favorecendo a dinâmica fonte-sumidouro.

Nossos resultados indicam de que a estratégia de conservação da fauna aliada a conservação técnicas de manejo de populações tradicionais tem sido eficaz nas RDSs Mamirauá e Amanã. Diante do cenário atual de crescente pressão sobre a floresta amazônica pela expansão da agricultura, pecuária e garimpo, além do aumento da frequência de eventos climáticos extremos, nossos resultados indicam a importância fundamental das áreas protegidas e o importante papel das reservas de uso sustentável, quando bem geridas, como um caminho para a conservação e sustentabilidade na Amazônia.