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

# EFEITOS DO FOGO NAS COMUNIDADES DE AVES EM FLORESTAS SAZONALMENTE ALAGADAS AO LONGO DE RIOS DE ÁGUA PRETA AMAZÔNICOS NA BACIA DORIO NEGRO

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MANAUS, AM FEVEREIRO, 2024 **CLEITON VALENTIM** 

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# Sinopse:

Estudou-se o impacto do fogo sobre as comunidades de aves em igapós da bacia do Rio Negro, no noroeste da Amazônia. Foram analisados os efeitos do fogo ocorridos em diferentes intervalos de tempo no passado e avaliado seus efeitos sobre a riqueza e composição de espécies de aves, considerando também a estrutura da vegetação, como densidade e abertura do dossel.

Palavras-chave: Igapó, composição de aves, riqueza de aves, fogo, Amazônia.

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"Podemos permitir que satélites, planetas, sóis, universo, ou melhor, sistemas inteiros do universo, sejam governados por leis, mas o menor inseto, desejamos que seja criado imediatamente por um ato especial" – Charles Darwin

# RESUMO

Incêndios florestais antropogênicos têm modificado florestas tropicais a níveis alarmantes e, com o aumento de eventos extremos impulsionados pelas mudanças climáticas, os incêndios se tornarão cada vez mais frequentes. Na Amazônia as florestas sazonalmente inundadas por rios de água preta (i.e., igapós), são altamente vulneráveis a incêndios. Apesar de apresentar diversidade única e especializada, pouco se sabe sobre como o fogo afeta os organismos de ambientes alagáveis. Aqui investigamos a resposta da avifauna a incêndios em diferentes intervalos de tempo no passado em igapós da bacia do Rio Negro. Foram selecionados 57 sítios de amostragens distribuídos em áreas controle, de queimadas recentes (2013 a 2022) e de queimadas antigas (1984 a 2003). Utilizamos gravadores autônomos para o registro das espécies de aves. Ainda, coletamos informações sobre a densidade da vegetação e abertura do dossel para cada sítio. Registramos 186 espécies de aves, sendo que igapós queimados recentemente apresentaram a maior riqueza, enquanto que os controles e os de queimadas antigas, apresentaram riqueza semelhante. A composição de especies de aves foi diferente em todas as categorias de igapó, indicando que com o passar do tempo a composição de especies não se torna mais semelhante ao igapó não queimado. A densidade da vegetação apresentou pouco efeito sobre a composição e riqueza de espécies, enquanto que a abertura do dossel mostrou maior influência sobre a riqueza. Nossos resultados mostram que o fogo modifica a estrutura da vegetação, o que leva a mudanças na composição e riqueza de especies de aves. Mostramos que num período de 38 anos após o incêndio a composição de aves não se recupera. Esses resultados criam um alerta sobre a vulnerabilidade dessas espécies, e ressalta a urgência de medidas mitigatórias e de prevenção para incêndios futuros.

# ABSTRACT

Anthropogenic forest fires have been modifying tropical forests at alarming levels, and with the increase in extreme events driven by climate change, fires will become increasingly frequent. In the Amazon, forests seasonally flooded by blackwater rivers (i.e., igapós) are highly vulnerable to fires. Despite presenting unique and specialized diversity, little is known about how fire affects organisms in flooded environments. Here, we investigated the avifauna's response to fires at different time intervals in the past in igapós of the Rio Negro basin. Fifty-seven sampling sites were selected, distributed among control areas, recently burned areas (2013 to 2022), and old burn areas (1984 to 2003). We used autonomous recorders to document bird species and collected information on vegetation density and canopy openness for each site. We recorded 186 bird species, with recently burned igapós showing the highest richness, while controls and old burn areas exhibited similar richness. The bird species composition differed in all igapó categories, indicating that over time, the species composition does not become more similar to unburned igapós. Vegetation density had little effect on species composition and richness, while canopy openness showed a greater influence on richness. Our results demonstrate that fire alters vegetation structure, leading to changes in bird species composition and richness. We show that over a 38-year period after the fire, bird composition does not recover. These findings raise an alert about the vulnerability of these species and emphasize the urgency of mitigating and preventing measures for future fires.

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# Sumário

# INTRODUÇÃO

A Amazônia apresenta a maior extensão de cobertura de floresta tropical do planeta (ter Steege et al., 2020) e é responsável por desempenhar diversos serviços ecossistêmicos cruciais, como dos ciclos de água e carbono (Jung et al., 2021), e contribui para a mitigação das mudanças climáticas globais (Gatti et al., 2021). Ainda, abriga mais de 10% de todas as espécies de plantas e vertebrados do mundo (Guayasamin et al., 2021), sendo considerada a floresta mais diversa do planeta (Antonelli et al., 2018).

Essa diversidade pode estar associada a heterogeneidade dos ambientes amazônicos, uma vez que ambientes heterogêneos são conhecidos por terem uma relação positiva com a riqueza de espécies (Cramer & Verboom, 2017), pois oferecem uma gama maior de nichos a serem explorados (Tabarelli et al., 2010; Martins et al., 2022). Os grandes rios amazônicos, de modo geral, são um dos impulsionadores de tal heterogeneidade (Bueno et al., 2012; Pomara et al., 2014; Menger et al., 2017), já que modificam a paisagem com sua correnteza, cargas sedimentares e flutuações no nível da água (Junk et al., 2014), criando diferentes categorias de planícies de inundação (Junk et al., 2011; Fleischmann et al., 2022). Essas planícies inundadas, por sua vez, abrigam plantas (Wittmann et al., 2010; Parolin et al., 2013) e animais (Goulding et al., 1988; Adis et al., 2010) distintos e especializados (Remsen & Parker III, 1983; Haugaasen & Peres, 2005; Borges et al., 2014), além de espécies restritas somente a alguns desses ambientes (Cohn-Haft et al., 2007; Myster, 2016). Os rios também funcionam como barreiras biogeográficas, influenciando a dispersão, composição e abundância de espécies associadas às áreas não alagáveis (e.g. terra firme), assim como delimitadores de áreas de endemismo (Cracraft, 1985; Cohn-Haft et a., 2007; Borges & Silva, 2012; Ribas et al., 2012; Maximiano et al., 2020; Thom et al., 2020; Laranjeiras et al., 2019, 2021).

Florestas de planícies de inundação cobrem aproximadamente 15% de toda a bacia amazônica (Hess et al., 2015) e são constantemente afetadas por flutuações previsíveis e monomodais do nível da água (i.e. pulsos de inundação, Junk et al., 2014). Ademais, exercem papéis fundamentais na redução do avanço das mudanças climáticas (Strassburg et al., 2020) e são habitats-chave para muitas espécies de vertebrados, como peixes (Correa et al., 2015; van der Sleen et al., 2020), primatas

(Haugaasen & Peres, 2007; Paim et al., 2019) e aves (Beja et al., 2010; Rowedder et al., 2021) que utilizam essas florestas em algum estágio da vida.

De maneira geral, as florestas alagáveis são classificadas conforme a coloração da água dos rios que as banham que é resultado de fatores físico-químicos da água associados à geomorfologia das áreas de nascentes e percurso, e que influenciam a estrutura da vegetação (Sioli, 1956; Schöngart et al., 2010; Junk et al., 2011; Wittmann & Junk, 2016). Por exemplo, as áreas alagadas por rios de água branca (e.g. Rio Amazonas, Rio Madeira) – originários das terras baixas andinas, com grande quantidade de sedimentos ricos em nutrientes (Wittmann & Junk, 2016) – são conhecidas localmente como "várzeas", apresentam solos férteis, florestas com maior crescimento, e comunidades de plantas herbáceas altamente produtivas (Junk et al., 2011). Já florestas alagadas por rios de águas pretas (e.g. Rio Negro) – drenados da região dos escudos das Guianas (Latrubesse et al., 2005) e com baixa quantidade de material em suspensão – são chamados de "igapós" (Junk et al., 2011) que, quando comparados com as várzeas, apresentam baixa diversidade de espécies de árvores, além de serem regidos por processos dinâmicos lentos (Wittmann et al., 2010; Junk et al., 2015).

Atualmente, as áreas alagáveis estão entre os ecossistemas mais ameaçados do planeta (Junk et al., 2018). Barragens hidrelétricas, desmatamento e as mudanças climáticas são conhecidas por afetarem a dinâmica dessas florestas, alterando o regime natural de alguns rios (Schongart et al., 2021; Fleischmann et al., 2023) e ameaçando a diversidade biológica (Laranjeiras et al., 2019). Além disso, eventos de seca extrema têm tornado os incêndios florestais mais frequentes e intensos na Amazônia (Brando et al., 2014; Alencar et al., 2015; Barlow et al., 2018), e as florestas alagáveis em particular, apresentam uma sensibilidade muito maior a esses eventos quando comparada com outros tipos de floresta (Flores et al., 2017). Para as florestas de igapó, os efeitos são ainda mais drásticos (Resende et al., 2014; Flores et al., 2014, 2017; Schöngart et al., 2017), já que sua estrutura vegetal ligeiramente aberta (Almeida et al., 2016) facilita que o tapete de raízes fique descoberto e seque (Santos & Nelson, 2013), expondo a camada orgânica altamente inflamável do solo (Flores et al., 2016). Após um primeiro evento de fogo no igapó, devido a lenta recuperação dessas florestas sazonalmente inundadas, a estrutura do dossel, agora aberta, aumenta as chances de novos incêndios (Almeida et al., 2016; Flores et al., 2017) tornando o igapó queimado semelhante a savana em relação a estrutura da vegetação

(aberta) após queimadas sucessivas (Flores & Holmgren, 2021a). A permanência da cobertura do dossel em estado aberto pode ter importantes impactos na composição de espécies da fauna, já que a ausência de arvores pode reduzir a disponibilidade de frutos para espécies animais (Flores & Holmgren, 2021a), afetando assim a dispersão de sementes para plantas dependentes desse tipo de interação (Barlow et al., 2002; Barlow & Peres, 2004; Hawes et al., 2020; Weiss et al. 2023) e dificultando ainda mais a recuperação da floresta (Flores & Holmgren, 2021a).

As áreas mais afetadas pelo fogo são aquelas próximas a assentamos humanos, sugerindo que atividades antrópicas diretas podem ser também a fonte de ignição (Carvalho et al., 2021). Embora áreas remotas de florestas de igapó apresentem baixa probabilidade de incêndios naturais, eventos de seca extrema podem ser facilitadores para queimadas, como verificado, por exemplo, por Carvalho et al. (2021), que indicam que em igapós da bacia do baixo Rio Negro, mais de 92,4% das áreas queimadas estão associadas a eventos de El Niño.

Aproximadamente 15% das espécies de aves não aquáticas da Amazônia são consideradas especialista de ambientes alagáveis (Remsen & Parker III, 1983; Borges et al., 2019; Laranjeiras et al., 2019) e muitas parecem ser restritas a esses ambientes (Parker III et al., 1996; Cohn-Haft et al., 2007). Embora as aves sejam o grupo de vertebrados mais bem conhecido da Amazônia (Cohn-Haft et al., 2007), e que os estudos da avifauna de áreas alagáveis estejam aumentando (Borges & Almeida, 2011; Borges & Silva, 2012; Laranjeiras et al., 2019; Thom et al., 2020; Diniz et al., 2023), pouco se sabe sobre como as mudanças atuais estão afetando as espécies desses ambientes, em especial eventos de incêndios.

As aves podem fornecer insights interessantes sobre as trajetórias da comunidade em resposta a incêndios florestais, pois desempenham vários papéis e prestam serviços ecossistêmicos, como dispersão de sementes, polinização e predação (Sick, 1997; Whelan et al., 2008). Mudanças na composição de espécies de aves podem ocorrer em resposta a alterações na estrutura da vegetação causadas pelo fogo (Barlow et al., 2002; Hidasi-Neto et al., 2012). Na Amazônia, estudos que investigaram a avifauna no contexto de incêndios focaram mais em florestas não inundadas (ou seja, terra firme; Barlow et al., 2002, 2006; Barlow & Peres, 2004; Hidasi-Neto et al., 2012). Além disso, a resposta da comunidade de aves ao fogo em áreas de terra firme pode apresentar resultados contrastantes. Em relação

à riqueza, por exemplo, Peres et al. (2003) não encontraram mudanças significativas na riqueza de espécies de aves no sub-bosque de florestas queimadas e de controle na Amazônia Central. Por outro lado, Barlow et al. (2002), também em florestas de terra firme na Amazônia Central, identificaram maior riqueza de espécies em florestas não queimadas. Barlow e Peres (2004), além de encontrarem maior riqueza em florestas queimadas uma vez, também observaram que a abundância e composição de espécies de aves em florestas de terra firme na Amazônia mudam ao longo do tempo após o incêndio, tornando as áreas queimadas menos semelhantes às não queimadas. Ritter et al. (2012) encontraram resultados semelhantes para a avifauna das florestas de igapó na bacia do Rio Negro, no noroeste da Amazônia. Resultados diferentes na riqueza de espécies de aves também foram observados em estudos de cronossequência em florestas perturbadas por agentes diferentes do fogo. Borges et al. (2021) observaram que a riqueza de espécies de aves em florestas de terras firme modificadas pela agricultura no noroeste da Amazônia diminui à medida que a idade da floresta secundária aumenta, e em florestas perturbadas a mais tempo, a riqueza é semelhante à da floresta primária. Enquanto isso, Sayer et al. (2017) observaram que a riqueza de aves especialistas em florestas de terra firme aumenta com a idade de florestas secundárias impactadas pelo desmatamento para agricultura nos trópicos, estimando que a recuperação dessas florestas pode levar mais de 100 anos. Embora todos esses estudos tenham utilizado de rede de neblina para a coleta das espécies, os resultados apontam que a resposta da avifauna ao fogo, pode ser imprevisível.

# **OBJETIVO GERAL E HIPÓTESES**

O objetivo do presente estudo foi investigar o efeito do fogo nas comunidades de aves das florestas de igapó de água preta. Mais especificamente, comparamos a avifauna de locais não afetados pelo fogo nos últimos 38 anos, locais queimados recentemente (<10 anos) e locais queimados há mais tempo (10-20 anos). Buscamos compreender se a riqueza de espécies de aves aumenta, diminui ou permanece inalterada nos diferentes intervalos de tempo após o incêndio. Ainda, investigamos se, com o passar do tempo após o fogo, a composição de espécies se assemelha ou não ao igapó não queimado. Valentim, C.; Capurucho, J.M.G; Bobrowiec, P.E.D; Leite, G.; Martins, G.M.; Schöngart, J. & Ribas, C.C. 2024. Fire effects on bird communities from seasonally flooded forests along Amazonian black water rivers of the Negro River basin. Manuscrito submetido para *Diversity and Distributions*.

# Abstract

### Aim

Fire has been one of the events that most disrupt the coverage of tropical forests in the Amazon. Forests seasonally flooded by blackwater rivers (e.g., igapó) show an even greater vulnerability to fires, and because they harbor species of organisms specialized and adapted to the seasonal dynamics of water, the threat to this forest also jeopardizes these organisms. Birds can provide interesting insights into the effect of fire on the environment, as they provide essential ecosystem services. Here, we investigate how fire events at different time intervals affect the richness and species composition of birds in igapó forests.

# Location

Negro River basin, Northwest Amazon.

### Methods

We used autonomous recorders to survey bird species at 57 sampling points divided among control igapós (without a history of fire), igapós burned longer ago, and recently burned igapós. We compared the richness and species composition among the three igapó treatments and investigated how the vegetation structure affected by fire influenced the avifauna.

### Results

Recently burned igapós showed the highest species richness, while those burned longer ago had richness similar to control igapós. Species composition differed across all igapó categories, with turnover being the beta diversity component that most influenced compositional differences. Canopy closure was the vegetation structure that most influenced species richness.

#### Main conclusions

For at least 38 years after the fire, the igapó bird community appears not to recover, even though richness reaches values similar to control igapós. Species richness is negatively influenced by canopy closure. Birds from igapó forests seem highly vulnerable to fires, not returning to burned igapós even after 38 years. Urgent actions for fire monitoring and preservation of igapó remnants are essential.

Key-words: Autonomous recorders; composition; igapó; rainforest threats; species richness dynamics; turnover; vegetation structure.

# Resumo

#### Objetivo

O fogo tem sido um dos eventos que mais perturba a cobertura das florestas tropicais na Amazônia. As florestas sazonalmente alagadas por rios de água preta (por exemplo, igapó) mostram uma vulnerabilidade ainda maior aos incêndios e, por abrigarem espécies de organismos especializados e adaptados à dinâmica sazonal da água, a ameaça a essa floresta também coloca em risco esses organismos. As aves podem fornecer informações interessantes sobre o efeito do fogo no ambiente, pois oferecem serviços ecossistêmicos essenciais. Aqui, investigamos como os eventos de incêndio em diferentes intervalos de tempo afetam a riqueza e a composição de espécies de aves em florestas de igapó.

#### Localização

Bacia do Rio Negro, Noroeste da Amazônia.

# Métodos

Utilizamos gravadores autônomos para o levantamento das espécies de aves em 57 pontos de amostragem divididos entre igapós controle (sem histórico de fogo), igapós queimados há mais tempo no passado e igapós queimados recentemente. Comparamos a riqueza e a composição de espécies entre os três tratamentos de igapó e investigamos como a estrutura da vegetação afetada pelo fogo influenciou a avifauna.

# Resultados

Os igapós queimados recentemente mostraram a maior riqueza de espécies, enquanto aqueles queimados há mais tempo apresentaram riqueza semelhante aos igapós controle. A composição de espécies diferiu em todas as categorias de igapó, sendo a taxa de substituição o componente da diversidade beta que mais influenciou as diferenças composicionais. O fechamento do dossel foi a estrutura da vegetação que mais influenciou a riqueza de espécies.

#### Principais conclusões

Por pelo menos 38 anos após o incêndio, a comunidade de aves do igapó parece não se recuperar, mesmo que a riqueza atinja valores semelhantes aos dos igapós controle. A riqueza de espécies é negativamente influenciada pelo fechamento do dossel. As aves das florestas de igapó parecem ser altamente vulneráveis aos incêndios, não retornando aos igapós queimados mesmo após 38 anos. Ações urgentes para monitoramento de incêndios e preservação de remanescentes de igapó são essenciais.

Palavras-chave: ameaças à floresta tropical; composição; dinâmica de riqueza de espécies; estrutura da vegetação; gravadores autônomos; igapó; substituição de espécies.

### Introduction

Tropical rainforests are threatened by anthropogenic activities at an alarming rate (FAO, 2020). These activities modify land cover, causing loss and fragmentation of forests, degradation of their remnants, and affect community diversity and composition (Matuoka et al., 2020; Melo et al 2021; Faria et al., 2023). Forest fires are increasingly responsible for forest disturbances, and their occurrence tends to increase with more extreme seasonality (Erfanian et al., 2017).

In general, stages of forest succession after disturbance are characterized by changes in vegetation structure, as well as in vegetation species composition (Worbes et al., 1992; Wittmann et al., 2004; Silva et al., 2016). In the early stages of succession, the forest is dominated by pioneer species adapted to disturbances (Pontes-Lopes et al., 2021). As the forest establishes, the availability of light, water, and nutrients tends to decrease (Poorter et al., 2019), and consequently, pioneer species are replaced by those better adapted to more stable environments (van Breuguel et al., 2013). The succession process can be shaped by various factors such as water availability, soil, and climate characteristics, landscape structure as well as the intensity of management (ter Steege et al., 2006; Becknell et al., 2012; Lohbeck et al., 2013; Becknell & Powers, 2014; Jakovac et al., 2016; 2021; Longo et al., 2016).

The Amazon, the largest tropical forest on the planet (ter Steege et al., 2020), hundreds of hectares of forest are lost every day (INPE, 2019) and converted for agriculture (He et al., 2021), mining (Sonter et al., 2017), and livestock (Ferrante & Fearnside, 2022), or flooded for hydroelectric dam construction (Covey et al., 2021; Melo et al., 2021). Additionally, driven by global climate change, a significant portion of the Amazon is facing extreme changes in rainfall patterns (Xu et al., 2020). The impacts of fire can vary due to the intensity and frequency of fire, as well as the composition and structure of pre-fire vegetation (Silva et al., 2005). Forest fires increase tree mortality in the Amazon basin as species are not adapted against this disturbance (Brando et al., 2014), changing and simplifying vegetation structure (Barlow et al., 2019; Xu et al., 2020). Fire also tends to reduce canopy coverage, increasing the amount of light entering the forest (Peres et al., 2003; Almeida et al., 2016) and thus the chances of new fires (Resende et al., 2014), which can slow down forest regeneration time (Flores & Homgren et al., 2021b).

Amazonian forests that are seasonally flooded by blackwater rivers (i.e., igapós, Junk et al., 2011) are highly vulnerable to fires (Resende et al., 2014; Flores et al., 2014, 2017; Schöngart et al., 2017). The occurrence of El Niños coincides with the non-flooded period of the igapó, generating a huge climatological water deficit as rainfall reduces and temperature increases which enhances potential evapotranspiration (Carvalho et al. 2021). Soils in the igapó have a high fraction of fine sand, which leads to a low water storage capacity (Wittmann et al. 2022). The longterm flooding and nutrient-poor soils result to a lower canopy height of the forests and the absence of understory causes a drier microclimate inside the forest (Almeida et al. 2016). Due to the long anoxic conditions during flooding and the oligotrophic soil conditions, mats of fine roots on the soil surface or near it and slow decomposition of organic matter result to an accumulation of fine fuel (Santos & Nelson, 2013). The severe hydroclimatic drought conditions induced by El Niño are coupled with specific characteristics of the igapó turning this ecosystem highly vulnerable to fires. However, fire ignition is mainly anthropogenic caused by fire escapes from slash-and-burn activities in adjacent terra firme forests near to human settlements or not extinguished campfires on the river margin (Ritter et al. 2012, Carvalho et al., 2021). Fires in igapó forests can cause mortality of up to 90% of trees (Flores et al., 2014), and, due to the slow recovery when compared to non-flooded forest (terra firme), vegetation structure may remain altered for a period of 10 to 20 years after the fire (Flores et al., 2017), increasing the chances of new fires (Almeida et al., 2016; Flores et al., 2017).

The long-term persistence of open canopy can have significant impacts on animal species composition (Barlow et al., 2002). Since fire promotes environments with fewer tree species, it can also lead to a decrease in animal diversity (Barlow et al., 2002; Barlow & Peres, 2004; Ritter et al., 2012; Hawes et al., 2020). However, studies of chronosequences that have investigated the long-term effects of fire remain scarce (Brando et al., 2014; Silva et al., 2018; Andrade et al., 2020, Coelho et al., 2023), and those few studies provide limited information on vegetation structure changes and regeneration after the fire events (but see Pontes-Lopes et al., 2021) and on how the fauna responds to these changes (Barlow et al., 2002; Barlow & Peres, 2004; Ritter et al., 2012).

Birds can provide interesting insights about community trajectories in response to wildfires as they play various ecological roles and provide ecosystem services, such as seed dispersal, pollination, and predation (Sick, 1997; Whelan et al., 2008). Changes in bird species composition may occur in response to changes in vegetation structure caused by fire (Barlow et al., 2002; Hidasi-Neto et al., 2012). In the Amazon, studies that have investigated avifauna in the context of fires have focused more on non-flooded forests (i.e., terra firme; Barlow et al., 2002, 2006; Barlow & Peres, 2004; Hidasi-Neto et al., 2012), while information for seasonally flooded areas is scarce (Ritter et al., 2012). Additionally, the responses of the bird community to fire can present contrasting outcomes. Regarding richness, for example, Peres et al. (2003) found no significant changes in the understory bird species richness in burned and control sites in terra firme forests in Central Amazon. On the other hand, Barlow et al. (2002), also in terra firme forests of Central Amazon, identified higher species richness in unburned forests. Barlow and Peres (2004), besides finding higher richness in forests burned once, also observed that the abundance and species composition of birds in *terra firme* forests in the Amazon change over time after the fire, causing burned areas to become less similar to unburned ones. Ritter et al. (2012) found similar results for the avifauna from igapó forests in the Negro River basin in Northwest Amazon. Furthermore, Coelho et al. (2023), in Amazonian savannas, observed consistent effects of fire on bird community composition across various temporal and spatial scales. Their findings revealed an increase in forest species in less disturbed areas.

Different results in bird species richness have also been observed in chronosequence studies in forests disturbed by agents other than fire. Borges et al (2021) noted that bird species richness in upland forests modified by agriculture in the northwest Amazon decreased as the age of secondary *terra firme* forest increased, and in longer undisturbed forests, the richness was similar to that of primary forest. Meanwhile, Sayer et al. (2017) observed that the richness of forest-specialist birds increases with the age of secondary forests impacted by deforestation for agriculture in the tropics, estimating that the recovery of these forests may take more than 100 years.

In this study, we investigated the effect of fire in black water's igapós on the bird communities from the Negro River basin, northwestern Amazonia, Brazil. More specifically we compared the avifauna from sites not affected by fire in the last 38 years, recently burned sites (<10 years), and sites burned a longer time ago (20-40 years). Based on previous results on bird communities of Amazonian forests affected by fire, we expected to find similar or smaller species richness in burned sites when

compared to control sites. We also investigated if there is a difference in the bird communities of sites affected by fire at different moments in the past and tested if, with increasing time after burning, bird species composition would become more or less similar to control sites.

# Methodology

#### Study area

The Negro River basin has a catchment area of approximately 712,000 km<sup>2</sup> (Junk et al., 2015), and around 12.1% of its basin is composed of seasonally flooded igapó forests, with tree coverage exceeding 85% (Melack & Hess, 2010). The region is characterized by annual, regular and predictable flood pulses with annual amplitudes varying between 6 and 10 m (Junk et al., 2015). We sampled 57 sites along the rivers Cuiuni, Jaú, Negro, and Unini in the lower and middle portions of the Negro River basin, northwestern Amazon. Based on analyses of Landsat data for the region (Carvalho et al. 2021, Flores & Holmgreen, 2021a), sample sites were divided into three categories: original igapó – without past fire occurrence in the last 38 years, considered as control sites; recent fire - sites that burned between 2013 and 2022; and old fire - sites that burned between 1984 and 2003 (Fig. 1). In the Jaú River, six control sites, 12 recent fire sites, and four old fire sites were sampled. For the Unini River, six control sites, four recent fire sites, and 10 old fire sites were sampled. The Cuiuni and Negro rivers had each three control sites, and four and five recent fire sites, respectively. The selection of sampling sites in the Jaú and Unini rivers was based on the study by Carvalho et al. (2021), which mapped fire scars from 1983 to 2017 using remote sensing. We added two sites in the Jaú River that experienced fires in 2022. The igapós of the Cuiuni and Negro rivers (hereafter Barcelos locality) were selected following Flores and Holmgren (2021a) and were affected by fire events in the years 2015 and 2016.

Bird occurrence data

The sampling of bird species occurrence was performed between October and November 2022, during the dry season. We used passive acoustic monitoring with

autonomous portable recorders AudioMoth v.1.2.0 (LabMaker), equipped with a microphone with a range of up to 200 meters (Hill et al., 2017). For each sampling site, a recorder was placed at a height of 1.5 meters and programmed to record 1 minute every 10 minutes, throughout 24 hours, totaling 144 minutes of recording per day, at a frequency of 48 KHz (LeBien et al., 2020). Each recorder remained active for seven consecutive days at each sampling site.

For the identification of recorded bird species, we implemented the following protocol:

- We created a list of bird species with potential occurrence in the study area, following Borges and Almeida (2011) and Borges (2013). A total of 664 species were considered. We excluded species from the Apodidae, Cathartidae and Scolopacidae families as they exhibit very similar vocalizations and therefore could not be distinguished from each other following the procedures described in step (3);
- 2. For each species in the list, we searched for a recording of the most frequent model recording) Wikiaves or call (i.e., using the song (https://www.wikiaves.com.br/index.php) and Xeno-canto (https://xenocanto.org/) databases, and prioritizing recordings collected near or within the study area. We created templates based on species recordings, which involve extracting the sound signal from the recording corresponding to the species vocalization. One template was created for each species;
- 3. We implemented the Pattern Matching functionality of the RFCx ARBIMON platform (https://arbimon.rfcx.org) (LeBien et al., 2020) to determine the presence or absence of each species in the field-collected recordings. This function involves correlating similar acoustic signals between the recordings and the template generated above. We chose a detection threshold value of 0.1 to enhance species detectability, as suggested by LeBien et al. (2020) and Melo et al. (2021). We applied this method to analyze five randomly selected days of recordings from the seven days of sampling at each site. We only considered recordings made between 05:00 and 10:00 hours and between 16:00 and 18:00 hours, as they represent the periods of highest bird species activity, totaling 210 minutes per sampling site per day;
- 4. As a complementary approach, for the two days not analyzed using the Pattern Matching scheme, we identified bird species by listening to recordings from

each site, considering the early morning hours (05:00 to 07:00), and the early evening hours (18:00 to 20:00). We employed this supplementary method to include species with a larger vocal repertoire that may not have been identified with the Pattern Matching method. This approach also enabled us to include nocturnal species;

5. Based on the species identified in steps 3 and 4, we generated a per site species presence/absence matrix, following the taxonomy of the Brazilian Ornithological Records Committee (Pacheco et al., 2021). For species with very similar vocalizations, occurrence was grouped at the genus level.

Using the pattern matching strategy, a total of 11,970 minutes of recordings were analyzed across the 57 sampling sites. The complementary method resulted in 48 minutes of recording per sampling site (2,736 minutes sampled), amounting to 14,706 minutes of recordings evaluated across both methods.

# Vegetation structure

We collected two variables related to vegetation structure: canopy cover and vegetation clutter. To estimate canopy cover, we used the Gap Light Analysis Mobile App (GLAMA), an Android smartphone application that calculates the Canopy Cover Index (CCI) using field photos. We took four photos per site, one at each cardinal point (North, South, East, and West) at a distance of 5 m from the recorder, using a Xiaomi Redmi Note 8 smartphone placed horizontally at a height of 1.5 m from the ground. The CCI resizes hemispheric projections of canopy closure collected in the photographs to a perpendicular projection of light openings (Gonsamo et al., 2013). For each sampling site, we used the average CCI from the four photographs.

The vegetation clutter was measured using a 2.5-meter pole, graduated in black and white at 10 cm intervals, totaling 25 graduations, as proposed by Haugaasen & Peres (2006). The pole was kept vertically alongside the recorder. Then, at a distance of 5 m and at each cardinal point (North, South, East, and West), fully visible black segments – those not obstructed by vegetation structures such as leaves and small branches - were counted. We used the average of these four counts to estimate vegetation density. Data analysis

To compare the bird species composition among igapó categories (control, recent fire and old fire), we conducted a Principal Coordinates Analysis (PCoA) ordination using the 'pcoa' function with Cailliez correction from the ape package v.5.7.1 (Paradis & Schliep, 2019). We employed the Jaccard dissimilarity index to obtain dissimilarity values between sites using the 'vegdist' function from the vegan package v.2.6.4 (Oksanen et al., 2022). The bird species composition for each igapó category (control, recent fire, and old fire) was compared using Generalized Linear Models (GLM) (Wang et al., 2012). We employed negative binomial GLMs in the 'manyglm' function (Warton et al., 2012) of the mvabund package v.4.2.1 (Wang et al., 2012, 2020) with sets of all species as response variables and the three igapo categories as predictor variables. The model-based approach potentially reduces type I and II errors by allowing hypothesis testing without confounding location effects with dispersion effects in a multivariate space (Warton et al., 2012). Pairwise comparisons between igapó categories were assessed using the 'anova.manyglm' function in mvabund, based on Monte Carlo resampling model and Wald test. P-values were adjusted for multiple testing and estimated using 999 bootstrap interactions. We employed the same approach to compare bird species richness for each igapó category. However, for this comparison, we used bird species richness per site as the response variable.

To assess how the two components of  $\beta$ -diversity (species substitution and gains and losses of species) contribute to differences in species composition among treatments, we adopted the approach proposed by Cardoso et al. (2014), where  $\beta$ total corresponds to the sum of the species replacement and species richness ( $\beta$ total =  $\beta$ repl +  $\beta$ rich). To do this, we used the 'beta.multi' function based on Jaccard dissimilarity from the BAT package v.2.9.4 (Cardoso et al., 2015). We used only comparisons between pairs of treatments to represent the components of  $\beta$ -diversity.

We compared vegetation variables such as canopy closure and vegetation density among igapó categories by fitting Generalized Linear Mixed Models (GLMM) using the 'glmmTMB' function with a Gaussian distribution from the glmmTMB package v.1.1.8 (Brooks et al., 2017). This analysis aimed to examine the relationship between the response variable (i.e., vegetation variables) and the explanatory variable, in this case, igapó categories, while considering the random effect of rivers. Using the

'Ismeans' function from the emmeans package v.1.8.9 (Lenth 2016), adjusted means were calculated for different igapó categories, with Tukey (HSD) tests for multiple comparisons.

Finally, we assessed the significance of canopy closure and vegetation clutter, both our predictor variables in this case, on the richness and composition of bird species using Generalized Linear Models (GLM). Firstly, we used the set of bird species as our response variable to obtain significance values of vegetation structure on bird species composition for each of the igapó categories. Subsequently, we used the richness values for each of the igapó categories. To obtain significance values, we utilized the 'anova.manyglm' function in mvabund, based on Monte Carlo model resampling and Wald test. P-values were adjusted for multiple testing and estimated using 999 bootstrap interactions.

#### Results

We recorded 186 bird species, of which five were identified at the genus level. The species were distributed across 42 families. Tyrannidae was the family with the highest number of species (n = 23), followed by Thamnophilidae, Thraupidae (n = 12), Dendrocolaptidae, and Psittacidae (n = 10) (Table S4). The most frequently recorded species at the sampling sites were *Amazona farinosa* (55 sites, 96.5%), followed by *Patagioenas cayennensis* (n = 50, 87.7%), *Amazona festiva* (n = 46, 80.7%), and *Dendroplex picus* and *Ramphastos tucanus* (n = 45, 79%). Species with a single record accounted for 21% of total number of species (39 species). Only 15 species were relatively ubiquitous, occurring in more than half of the sites.

The bird species composition differed among all treatments (control, recent fire and old fire, Table 1), with the greatest difference in species composition between control and recent fire sites (Fig. 2). The number of species was higher in sites with recent fires ( $39.9 \pm 2.74$  species) compared to control ( $32.8 \pm 2.87$  species) and sites with old fires ( $32.6 \pm 3.17$  species). However, the number of species was similar between control and old fire sites (Table 1). Total  $\beta$ -diversity was high and varied little between comparisons of the three treatments ( $\beta$ total = 0.72-0.76; Fig. 3). Total  $\beta$ diversity was driven mainly by the species substitution component (Table S1), with higher values in the comparison between control and recent burns sites ( $\beta$ repl = 0.62; Fig. 3). Canopy closure differed among the three treatments (Table S2 and S3; Fig. S1 b), with less closure in the recent burn treatment. The vegetation clutter differed only between the control treatment and the other treatments (Table S2 and S3; Fig. S1 a), with higher values in the control treatments. Bird species composition was influenced by canopy closure (Fig. S2), but not by vegetation clutter (Table 2). Species richness was negatively influenced by canopy closure, but not by vegetation clutter (Table 2 and S3, Figure 4). Canopy closure was the only variable influencing species composition in the recent burn treatment (Fig. S3) and with a marginal influence in species richness (Table 3).

# Discussion

Our study shows how the occurrence of fire affects bird communities in seasonally flooded igapó forests of the Negro River basin, Northwestern Amazonia. Igapós affected by recent wildfires (between 2013 and 2022) exhibited higher species richness compared to control sites and to sites impacted by fires longer ago (between 1984 and 2003). Although species richness was similar between control sites and sites affected by old fires, species composition was significantly different. The variation in bird  $\beta$ -diversity was primarily explained by species turnover (replacement), indicating that each of the three treatments had a distinct set of species. Canopy closure influenced species composition and richness, while vegetation clutter showed no effect. In sites affected by recent fires there was a negative relationship between species richness and canopy closure, with significant changes in species composition.

The effects of fire on bird species richness

We found the highest bird species richness in recently burned igapós, while richness was similar in igapós burned longer ago and control areas. Although distinct studies have revealed contrasting results regarding the effect of fire in bird communities, our results were similar to those of Barlow and Peres (2004) and Hidasi-Neto et al. (2012) for upland Amazonian forests, in which richness was higher in burned areas than in unburned environments. Peres et al. (2003) also reported that the overall species richness of understory birds in upland environments in the Amazon was not affected by wildfires. As the burned vegetation dies and the canopy becomes more open, species specialized on igapó environments (e.g., *Myiopagis flavivertex* and *Pipra filicauda*) are lost, while open-habitat generalists (e.g., *Cacicus cela* and *Pitangus sulphuratus*) and those specialized in open environments (e.g., *Progne tapera*) occupy the burned igapó. As the forest regenerates, species associated to open-habitats leave, and forest specialists take their place. Thus, the lower species richness in igapós with old fires, which becomes similar to the richness of unburned igapós, might be the result of environmental filtering. Borges et al. (2021) found a similar pattern for secondary upland forests in the Amazon, as species richness of birds in these secondary forests decreased with age, and older secondary forests had similar richness to that of primary forests. Here we may have identified a similar process for igapó forests, where the regeneration of the igapó forest may be filtering species associated to open environments, leading to a decrease in species richness.

#### Bird community composition changes driven by fire

Species composition differed among the three treatments, consistent with findings in other studies for upland forests (10 to 15 months, Barlow et al., 2002; Barlow & Peres, 2004) and flooded forests (Ritter et al., 2012) in the Amazon. Birds from flooded forests are reported to avoid upland forests, likely due to competition with other species (Rowedder et al., 2021). The rapid change in habitat structure and food resources caused by fire could drive the displacement of these species to upland forests or adjacent igapos, increasing competition in these adjacent environments and eventually local extinctions. As the tree structure regenerates in the igapó forest, some igapó specialists are no longer present in the surrounding area, and upland forest specialists begin to inhabit this secondary igapó forest, preventing the community of returning to a composition similar to unburned igapós (Rowedder et al., 2021).

The species turnover ( $\beta$ -repl) between treatments is the main component of  $\beta$ diversity variation. In the igapós, fire events could kill more than 90% of tree species that are not adapted to forest fires (Flores et al., 2014; Resende et al., 2014). Generally, fire event dramatically changes vegetation (Flores & Holmgren, 2021b), replacing fire-sensitive species with more tolerant ones (Silva et al., 2018). This replacement is observed in bird species composition as well. A total of 16 bird species were found only in unburned igapó forests. Species such as *Schiffornis major*, *Myiopagis flavivertex*, and *Pipra filicauda* are considered exclusive to igapós (Remsen & Parker, 1983; Borges & Carvalhaes, 2000; Borges & Almeida, 2011; Borges et al., 2014) and were not found in other treatments. *Paroaria gularis* was found only in the old fire treatment and is sometimes associated with igapó forests (Borges et al., 2014), as well as to anthropized vegetation (Borges & Carvalhaes, 2000; Borges & Almeida, 2011). Recent fire treatments presented 46 species that only occurred in this environment, many of these usually found only in upland forests (e.g. *Crypturellus variegatus, Tolmomyias assimillis, Trogon rufus*), open areas (e.g., clearings and white-sand ecosystems; *Elaenia flavogaster, Hydropsalis cayennensis*), and generalists tolerant to disturbed environments (e.g. *Butorides striata, Cercomacroides tyrannina, Philohydor lictor, Progne chalybea*) (Remsen & Parker, 1983; Borges & Carvalhaes, 2000; Borges & Almeida, 2011; Borges et al., 2014). These data highlight that igapó specialist birds show high sensitivity to fires, and their re-establishment over time after the fire is uncertain, making the conservation of these species critical.

Flores and Holmgren (2021a) indicate that the soil composition and tree species after forest fires in seasonally flooded forests change together, making these forests similar to white-sand ecosystems within 40 years, and this effect intensifies with the recurrence of fire. Here, we show a strong species turnover effect in different igapó treatments, but we cannot assert that such turnover over time after the fire leads to a bird species composition similar to bird communities found in white sand ecosystems. Testing this trend for bird communities may be challenging, given that, compared to the dominant terra firme upland forest habitat, igapó forests and other open vegetation formations may already have a more similar avifauna (Borges et al., 2014). For example, we recorded only one species considered as a specialist of white-sand ecosystems (Borges et al. 2016), Hydropsalis cayennensis, in a burned igapó site. Therefore, the hypothesis of a substitution of bird communities typical of igapó environments by those characteristics of white-sand ecosystems was not supported by our results. Furthermore, the presence of some species in common between burned igapós and open environments, like white-sand ecosystems, may be due to sharing the same disturbance-tolerant and/or open habitat specialist species attracted by the open vegetation structure, rather than necessarily due to the arrival of specialists of white-sand ecosystems (Borges et al., 2016).

Vegetation structure and the avifauna in igapós affected by fire

Feitoza et al. (in prep.), in black water igapó, found that over a chronosequence of 40 years after the fire, the height, basal area, and biomass of vegetation increase, resulting in a decrease in herbaceous cover due to shading. In the sites studied here, igapós affected by recent fires were predominantly composed of herbaceous plants and often lacked any canopy cover (pers. obs.). In contrast, igapó areas burned longer ago, despite the presence of herbaceous plants, already exhibited a more structured canopy (pers. obs.). This may suggest that, over time, regenerating igapós do not resemble unburned ones concerning the plant species composition (Flores & Holmgren, 2021a). There seems to be a unique species replacement process caused by fire, so that in the initial years after the fire event, canopy cover changes dramatically to a more open configuration dominated by herbaceous plants, also altering vegetation clutter (Almeida et al., 2016; Smith et al., 2023). Even with the woody plants establish, vegetation clutter takes a different path from the original, likely due to a different composition of plant species.

Canopy closure was significantly different between recently burned igapós and the other treatments. In upland forests in the central Amazon, Barlow et al. (2002) found similar results, with forests experiencing recent fires (<15 months) showing four times greater canopy openness or, in other words, reduced canopy closure, when compared to unburned forests. In burned igapó forests, Almeida et al. (2016) and Smith et al. (2023) observed a decrease in canopy closure compared to upland forests that had experienced fires, showing that the impact on vegetation structure could be even higher in seasonally flooded forests (Resende et al. 2014, Carvalho et al. 2021). Furthermore, burned igapós experienced the greatest impacts on other vegetation structure metrics compared to terra firme (e.g., leaf area; Smith et al., 2023). The reduced canopy cover caused by fires can accelerate erosion processes due to heavy rains, reducing soil fertility and tree growth rates (Flores et al., 2020). These combined effects maintain the forest structure in an open state, increasing the likelihood of new fire incidents (Resende et al., 2014). After a second fire event, the recruitment of new plants and the seed bank are more intensely affected, entering a feedback loop of open state (Flores & Holmgren, 2021b), potentially delaying the forest succession process.

Over time, in a forest succession process, open areas, light availability, water, and nutrient availability usually tend to decrease (Poorter et al., 2019), and the

complexity of the forest begins to establish itself, favoring species diversity and canopy structure (Martins et al., 2022). However, forest recovery can be influenced by various factors, such as the arrival of tree seeds from other environments, depending on the size of the affected area (Chazdon, 2003). Floodplain trees in the Amazon synchronize fruit maturation with the annual flooding season, whereas in non-flooded environments, fruiting occurs during the dry season (Haugaasen & Peres, 2007). This asynchrony in fruit production between flooded and non-flooded habitats creates an opportunity for frugivores to switch between environments when fruits are not available in one of them (Correa et al., 2022). Thus, the death of igapó trees caused by fire can harm not only the species exclusive to this environment but also frugivorous ones that rely on the asynchrony of fruiting and the access to igapó tree fruits when food becomes scarce in the upland forest. Few frugivorous bird species were detected in our data across all igapó treatments. While this may be a combined effect of seasonality and fire impact, as we sampled in the dry season, when bird species could be mostly foraging in upland forests, it is important to consider that the absence of frugivorous birds may add to the previous factors in delaying recovery of igapó vegetation after fire.

Contrastingly, we detected a high number of insectivore birds in igapós subjected to recent fires. In this case, the environmental change caused by the fire may function as an environmental filter, extinguishing forest specialists and making room for generalists tolerant to altered environments (Barlow & Peres, 2004, 2008), typically insectivores from open areas, such as tyrant flycatchers. This process may also contribute to biotic homogenization, eliminating unique avifaunas characteristic of specific Amazonian habitats (Silva et al., 2018). However, to understand if species homogenization indeed occurs, at least in terms of guild, it is important to investigate igapós also during the flooding season.

Several studies have shown that fire has a different impact on each species (Barlow et al., 2002; 2006; Barlow & Peres, 2004) or bird guild (e.g., arboreal insectivores, Barlow et al., 2002). In addition, the composition of the surrounding landscape matrix can also influence the recovery of vegetation in igapó forests subjected to fire and, consequently, the associated bird community. For example, unburned igapós near those that burned may serve as a source of igapó species to the affected areas as the forest recovers. Beja et al. (2010) observed that the structuring of bird communities is not only driven by the seasonal dynamics of floods and droughts, but the effect of this dynamic is influenced by the spatial configuration

of the forest. Thus, in the long term the impact of fire events on bird communities may also be influenced by landscape configuration. The intensity (Barlow & Peres, 2004) and recurrence of fire (Flores & Holmgren, 2021b) can also play a significant role in bird communities. More severe fires, often instigated by extreme climatic events (e.g., El Niño, Carvalho et al., 2021), are known to affect vegetation structure, and consequently bird communities, more intensely (Flores et al., 2014) (Barlow & Peres, 2004; Hidasi-Neto et al., 2012). The same happens with the occurrence of new fires in areas previously impacted by fire, where the persistent open state of vegetation limits the number of perches for bird species, and the loss of both the seed bank and bird dispersers hinders the establishment of fruit-bearing trees (Flores & Holmgren, 2021b). In this sense, it is important that parameters of fire intensity and frequency be considered in accessing the long-term threats to igapó ecosystems.

# Conclusion

Our results show that fire has a significant effect on igapó bird community structuring, and over time, for at least 38 years after the fire, the bird community does not return to the original structure. Also, measures of absolute species richness alone are not a good proxy of the integrity of environments, as we have shown increase in species richness after severe environmental impacts caused by fire. Bird communities affected by fire, although more species rich, are dominated by generalist, widespread and open area adapted species, contributing to biotic homogenization and loss of overall Amazonian diversity and uniqueness. More complex and nuanced measures of impact and recovery are needed for unique ecosystems that harbor specialized biota, as the seasonally flooded Amazonian forests.

Floodplain forests are among the most threatened environments on the planet (Junk et al., 2014). Their contribution to Earth's climate regulation (Santos et al., 2019), rainfall patterns, water storage (Junk et al., 2014), livelihoods for riparian communities (Fleishmann et al., 2023), and biodiversity (Remsen & Parker III, 1983; Borges & Carvalhaes, 2000; Haugaasen & Peres, 2005; Cohn-Haft et al., 2007; Wittmann et al., 2010) is at risk due to anthropogenic impacts. Global climate change may make fire events much more frequent in flooded forests (Resende et al., 2014; Carvalho et al., 2021). Thus, species dependent on seasonally flooded igapó forests also face a severe risk of extinction as climate events and fires become more intense and frequent

(Brando et al., 2020; Carvalho et al., 2021; Reis et al., 2021). After a fire, floodplain forests can still recover (Flores & Holmgren, 2021b). However, with the recurrence of new fires, recovery will likely depend on active restoration efforts (Flores & Holmgren, 2021a).

Efforts should focus on preventing fires from reaching these environments (Carvalho et al. 2021) and establishing global public policies to combat greenhouse gas emissions into the atmosphere to slow down planetary warming. In addition, seasonally flooded forests that have been burned should be monitored and protected against new fires (Flores & Holmgren, 2021a). For areas of forest burned multiple times, active restoration and establishment of connectivity corridors to unburned igapós may be necessary for recovery. These measures are only possible through the involvement of local Amazonian communities in the management of seasonally flooded areas, thus investment in socio-environmental actions is essential to prevent flooded forests and the species and ecosystem services depending on them from collapsing.

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# Tables

**Table 1**. Results from multivariate Generalized Linear Model (GLM) comparing the composition and species richness among the unburned igapó forests (control sites), recent fire (igapó burned from 2013 to 2022), and old fire (igapó burned from 1984 to 2003) in the Negro River basin, Northwestern Brazilian Amazon. P < 0.05 are in bold.

Response variable	Control × Recent fire		Control × Old fire		Recent fire × Old fire	
Response variable -	Z	Р	Z	Р	Z	Р
Species composition	455.5	0.001	229.9	0.001	270.0	0.001
Richness	15.9	0.001	0.49	0.48	8.70	0.006

**Table 2**. Generalized Linear Model (GLM) results for the relationship between bird species composition and richness and predictor variables canopy closure and vegetation clutter in all treatments of seasonally flooded forest by blackwater rivers (igapó) in the Negro River basin, Northwest Brazilian Amazon.

	Canopy	/ closure	Vegetation clutter	
Environmental variables —	Z	Р	Z	Р
Species composition	18.58	0.001	10.75	0.96
Richness	4.37	0.001	0.33	0.75

**Table 3**. Result from multivariate Generalized Linear Model (GLM) analyses of the composition and species richness of bird species correlation with canopy closure and vegetation clutter in the unburned igapó forest (control sites), recent fire (igapó burned from 2013 to 2022), and old fire (igapó burned from 1984 to 2003) in the Negro River basin, Northwestern Brazilian Amazon. P < 0.05 are in bold.

	Canopy	/ closure	Vegetation clutter	
Response variable	Z	Р	Z	Р
Control				
Species composition	8.07	0.87	8.95	0.44
Richness	0.026	0.98	0.538	0.61
Recent fire				
Species composition	12.21	0.001	10.11	0.87
Richness	1.81	0.059	1.199	0.23
Old fire				
Species composition	5.63	1.00	6.81	0.99
Richness	0.799	0.49	1.117	0.26

# Figures



**Figure 1**. Spatial distribution of the 57 sampling sites along the Negro, Cuiuni, Jaú and Unini rivers, Northwestern Brazilian Amazon, categorized into unburned igapó forests

(control sites, blue circles), recent fire (igapó burned from 2013 to 2022, red circles), and old fire (igapó burned from 1984 to 2003, orange circles).



**Figure 2**. Principal Coordinates Analysis (PCoA) ordination of bird assemblages sampled in the: unburned igapó forest (control sites; green circles); recent fire (igapó burned from 2013 to 2022; red circles); and old fire (igapó burned from 1984 to 2003; orange circles) in the Negro River basin, Northwestern Brazilian Amazon. Values in parentheses represent the percentage explained by each axis of the PCoA.



**Figure 3**. Variation in the components of  $\beta$ -diversity of bird assemblages among the unburned igapó forest (control sites), recent fire (igapó burned from 2013 to 2022), and old fire (igapó burned from 1984 to 2003) in the Negro River basin, Northwestern Brazilian Amazon. Horizontal lines represent the means, bars represent the 95% confidence intervals, and vertical lines indicate the maximum and minimum values. Black dots indicate extreme values. Dark gray:  $\beta$ total, total  $\beta$ -diversity; light blue:  $\beta$ repl,  $\beta$ -diversity related to species replacement (turnover); dark blue:  $\beta$ rich,  $\beta$ -diversity related to species (nestedness).



**Figure 4**. Bird species richness in the unburned igapó forest (control sites) (blue circles), recent fire (igapó burned from 2013 to 2022) (red circles), and old fire sites (igapó burned from 1984 to 2003) (orange circles) (a), with average richness for each treatment shown as a black circle; and the relationship between site richness and vegetation clutter (b) and canopy closure (c). In the regression plots, gray areas around the linear trend lines represent 95% confidence intervals.

# Suplementary material

**Table S1**. Comparation of components of  $\beta$ -diversity of bird assemblages among the three treatments of seasonally flooded forest by blackwater rivers (igapó) in the Negro River basin, Northwest Brazilian Amazon. Control (unburned igapó), recent fire (igapó burned from 2013 to 2022), and old fire (igapó burned from 1984 to 2003). Total Beta diversity ( $\beta$ total) = Beta replacement ( $\beta$ replc) + Beta richness ( $\beta$ rich).

Таха	Control x Recent fire	Control x Old fire	Recent fire x Old fire
βtotal	0.76	0.72	0.74
βreplc	0.62	0.52	0.49
βrich	0.15	0.19	0.25

**Table S2**. Results of the Mixed-effects Generalized Linear Model (GLMM) for the comparison of bird species richness, canopy closure, and vegetation clutter in the unburned igapó forest (control sites), recent fire (igapó burned from 2013 to 2022), and old fire (igapó burned from 1984 to 2003) in the Negro River basin, Northwest Brazilian Amazon. P < 0.05 are in bold.

Response variable	Control x Recent fire		Control x Old fire		Recent fire x Old fire	
	t	Р	t	Р	t	Р
Richness	-3.09	0.009	0.08	0.99	-2.66	0.028
Canopy closure	6.59	<0.0001	-0.06	0.99	5.22	<0.0001
Vegetation clutter	2.45	0.046	2.42	0.049	-0.39	0.92

**Table S3**. Results of the Generalized Linear Mixed Model (GLMM) for the LikelihoodRatio Test (LRT) for bird species richness parameters, canopy closure, and vegetationclutter.

Predictor variables	LRT	Р
Richness	10.80	0.005
Canopy closure	37.04	<0,0001
Vegetation clutter	7.59	0.023

**Table S4**. List of bird species recorded treatments of seasonally flooded forest by blackwater rivers (igapó) in the Negro River basin, Northwest Brazilian Amazon. Control (unburned igapó), recent fire (igapó burned from 2013 to 2022), and old fire (igapó burned from 1984 to 2003). Taxonomic nomenclature follows the Brazilian Committee of Ornithological Records (CBRO, Pacheco et al., 2021).

Ordem	Family	Specie	Control	Recent fire	Old fire	
Tinamiformes	Tinamidae	Tinamus major	x	x	х	
Tinamiformes	Tinamidae	Crypturellus cinereus		х		
Tinamiformes	Tinamidae	Crypturellus undulatus	х	х	х	
Tinamiformes	Tinamidae	Crypturellus variegatus		х		
Galliformes	Cracidae	Penelope jacquacu			х	
Galliformes	Cracidae	Pauxi tomentosa		х		
Columbiformes	Columbidae	Patagioenas speciosa	х	х	х	
Columbiformes	Columbidae	Patagioenas cayennensis	х	х	х	
Columbiformes	Columbidae	Patagioenas plumbea	х	х	х	
Columbiformes	Columbidae	Patagioenas subvinacea	х	х	х	
Columbiformes	Columbidae	Leptotila verreauxi	х	х	х	
Columbiformes	Columbidae	Leptotila rufaxilla	х	х	х	
Columbiformes	Columbidae	Columbina passerina		х		
Cuculiformes	Cuculidae	Crotophaga major		х		
Cuculiformes	Cuculidae	Crotophaga ani		х		
Cuculiformes	Cuculidae	Piaya cayana	х	х		
Nyctibiiformes	Nyctibiidae	Nyctibius griseus	х	х	х	
Caprimulgiformes	Caprimulgidae	Lurocalis semitorquatus	х	х	х	
Caprimulgiformes	Caprimulgidae	Nyctiprogne leucopyga	х	х	х	
Caprimulgiformes	Caprimulgidae	Nyctidromus nigrescens		х		
Caprimulgiformes	Caprimulgidae	Nyctidromus albicollis	х	Х	х	
Caprimulgiformes	Caprimulgidae	Hydropsalis cayennensis		х		

Apodiformes	Trochilidae	Florisuga mellivora			х
Apodiformes	Trochilidae	Phaethornis ruber	х	х	х
Apodiformes	Trochilidae	Chlorostilbon mellisugus	х	х	
Apodiformes	Trochilidae	Chrysuronia versicolor		х	х
Apodiformes	Trochilidae	Hylocharis sapphirina	х		
Apodiformes	Trochilidae	Chlorestes cyanus	х	х	
Gruiformes	Aramidae	Aramus guarauna		х	
Gruiformes	Psophiidae	Psophia crepitans	х		
Gruiformes	Heliornithidae	Heliornis fulica		х	х
Charadriiformes	Laridae	Phaetusa simplex	х	х	х
Eurypygiformes	Eurypygidae	Eurypyga helias	х	х	х
Pelecaniformes	Ardeidae	Tigrisoma lineatum	х	х	х
Pelecaniformes	Ardeidae	Cochlearius cochlearius		х	
Pelecaniformes	Ardeidae	Butorides striata		х	
Pelecaniformes	Ardeidae	Ardea sp.	х	х	х
Pelecaniformes	Threskiornithidae	Mesembrinibis cayennensis	х	х	х
Accipitriformes	Accipitridae	Busarellus nigricollis		х	
Accipitriformes	Accipitridae	Ictinia plumbea		х	х
Accipitriformes	Accipitridae	Rupornis magnirostris	х	х	х
Accipitriformes	Accipitridae	Leucopternis melanops		х	
Strigiformes	Strigidae	Megascops choliba	х	х	х
Strigiformes	Strigidae	Megascops watsonii	х		
Strigiformes	Strigidae	Pulsatrix perspicillata		х	х
Strigiformes	Strigidae	Strix virgata	х		
Strigiformes	Strigidae	Glaucidium brasilianum		х	х
Trogoniformes	Trogonidae	Trogon viridis	х	х	х
Trogoniformes	Trogonidae	Trogon curucui	х	х	х
Trogoniformes	Trogonidae	Trogon rufus		Х	

Trogoniformes	Trogonidae	Trogon collaris		х	
Coraciiformes	Alcedinidae	Megaceryle torquata	х	х	х
Coraciiformes	Alcedinidae	Chloroceryle amazona		х	х
Coraciiformes	Alcedinidae	Chloroceryle inda	х		
Galbuliformes	Galbulidae	Galbula albirostris	х	х	х
Galbuliformes	Galbulidae	Galbula leucogastra	х	х	х
Galbuliformes	Bucconidae	Chelidoptera tenebrosa		х	х
Galbuliformes	Bucconidae	Monasa nigrifrons	х	х	х
Galbuliformes	Bucconidae	Notharchus tectus	х		
Galbuliformes	Bucconidae	Notharchus hyperrhynchus		х	
Galbuliformes	Bucconidae	Tamatia tamatia	х	х	Х
Piciformes	Ramphastidae	Ramphastos tucanus	х	х	х
Piciformes	Ramphastidae	Ramphastos vitellinus	х	х	Х
Piciformes	Picidae	Picumnus sp.	х	х	х
Piciformes	Picidae	Melanerpes cruentatus	х	х	х
Piciformes	Picidae	Campephilus melanoleucos	х	х	х
Piciformes	Picidae	Dryocopus lineatus	х	х	х
Piciformes	Picidae	Celeus torquatus	х	х	Х
Piciformes	Picidae	Celeus undatus	х	х	Х
Piciformes	Picidae	Celeus flavus	х	х	Х
Piciformes	Picidae	Piculus flavigula	х		
Piciformes	Picidae	Colaptes punctigula	х	х	х
Falconiformes	Falconidae	Herpetotheres cachinnans		х	
Falconiformes	Falconidae	Ibycter americanus	х	х	Х
Falconiformes	Falconidae	Daptrius ater		х	
Falconiformes	Falconidae	Milvago chimachima		х	Х
Falconiformes	Falconidae	Falco sparverius		х	
Falconiformes	Falconidae	Falco rufigularis	х		

Falconiformes	Falconidae	Falco deiroleucus		х	
Psittaciformes	Psittacidae	Brotogeris sp.	х	х	Х
Psittaciformes	Psittacidae	Pyrilia barrabandi	х		Х
Psittaciformes	Psittacidae	Pionus menstruus	х	х	Х
Psittaciformes	Psittacidae	Amazona festiva	х	х	х
Psittaciformes	Psittacidae	Amazona farinosa	х	х	х
Psittaciformes	Psittacidae	Pionites melanocephalus		х	
Psittaciformes	Psittacidae	Eupsittula pertinax	х	х	Х
Psittaciformes	Psittacidae	Aratinga weddellii		х	
Psittaciformes	Psittacidae	<i>Ara</i> sp.	х	х	Х
Psittaciformes	Psittacidae	Psittacara leucophthalmus	х	х	Х
Passeriformes	Thamnophilidae	Myrmotherula obscura		х	
Passeriformes	Thamnophilidae	Myrmotherula cherriei	х	х	Х
Passeriformes	Thamnophilidae	Myrmotherula axillaris	х		
Passeriformes	Thamnophilidae	Myrmotherula assimilis	х	х	
Passeriformes	Thamnophilidae	Herpsilochmus dorsimaculatus	х	х	
Passeriformes	Thamnophilidae	Sakesphorus canadensis	х	х	Х
Passeriformes	Thamnophilidae	Thamnophilus amazonicus	х	х	Х
Passeriformes	Thamnophilidae	Hypocnemoides melanopogon	х	х	Х
Passeriformes	Thamnophilidae	Myrmoborus leucophrys	х		
Passeriformes	Thamnophilidae	Cercomacroides tyrannina		х	
Passeriformes	Thamnophilidae	Willisornis poecilinotus			Х
Passeriformes	Thamnophilidae	Gymnopithys leucaspis			х
Passeriformes	Formicariidae	Formicarius colma			Х
Passeriformes	Dendrocolaptidae	Sittasomus griseicapillus	х	х	Х
Passeriformes	Dendrocolaptidae	Dendrocincla fuliginosa	х	х	Х
Passeriformes	Dendrocolaptidae	Nasica longirostris	х	х	х
Passeriformes	Dendrocolaptidae	Dendrocolaptes radiolatus	х	х	х

Passeriformes	Dendrocolaptidae	Dendrocolaptes picumnus	х	х	
Passeriformes	Dendrocolaptidae	Xiphocolaptes promeropirhynchus	x	х	Х
Passeriformes	Dendrocolaptidae	Xiphorhynchus obsoletus	x	х	Х
Passeriformes	Dendrocolaptidae	Xiphorhynchus guttatoides	x	х	Х
Passeriformes	Dendrocolaptidae	Dendroplex picus	x	х	Х
Passeriformes	Dendrocolaptidae	Dendroplex kienerii	x	х	Х
Passeriformes	Furnariidae	Cranioleuca gutturata	x	х	
Passeriformes	Pipridae	Neopelma chrysocephalum	x		
Passeriformes	Pipridae	Heterocercus flavivertex	x	х	
Passeriformes	Pipridae	Pipra filicauda	x		
Passeriformes	Pipridae	Ceratopipra erythrocephala	x	х	Х
Passeriformes	Cotingidae	Cephalopterus ornatus		х	
Passeriformes	Cotingidae	Lipaugus vociferans		х	
Passeriformes	Tityridae	Schiffornis major	х		
Passeriformes	Tityridae	<i>Tityra</i> sp.	х	х	х
Passeriformes	Tityridae	Pachyramphus marginatus	х		
Passeriformes	Rhynchocyclidae	Tolmomyias sulphurescens	х	х	х
Passeriformes	Rhynchocyclidae	Tolmomyias assimilis		х	
Passeriformes	Rhynchocyclidae	Tolmomyias poliocephalus	х	х	х
Passeriformes	Rhynchocyclidae	Todirostrum maculatum	х	х	х
Passeriformes	Rhynchocyclidae	Todirostrum chrysocrotaphum	x	х	х
Passeriformes	Rhynchocyclidae	Hemitriccus minor	x	х	Х
Passeriformes	Tyrannidae	Zimmerius gracilipes	x	х	Х
Passeriformes	Tyrannidae	Inezia subflava	x	х	Х
Passeriformes	Tyrannidae	Camptostoma obsoletum	x	х	Х
Passeriformes	Tyrannidae	Elaenia flavogaster		х	
Passeriformes	Tyrannidae	Myiopagis gaimardii	x	х	х
Passeriformes	Tyrannidae	Myiopagis flavivertex	x		

Passeriformes	Tyrannidae	Tyrannulus elatus	х	х	х
Passeriformes	Tyrannidae	Phaeomyias murina	х	х	
Passeriformes	Tyrannidae	Attila cinnamomeus	х	х	х
Passeriformes	Tyrannidae	Legatus leucophaius		х	
Passeriformes	Tyrannidae	Ramphotrigon ruficauda	х	х	
Passeriformes	Tyrannidae	Myiarchus tuberculifer	х	х	х
Passeriformes	Tyrannidae	Myiarchus swainsoni	х	х	х
Passeriformes	Tyrannidae	Myiarchus ferox	х	х	х
Passeriformes	Tyrannidae	Myiarchus tyrannulus		х	х
Passeriformes	Tyrannidae	Rhytipterna simplex	х	х	х
Passeriformes	Tyrannidae	Pitangus sulphuratus	х	Х	х
Passeriformes	Tyrannidae	Philohydor lictor		Х	
Passeriformes	Tyrannidae	Myiozetetes cayanensis		Х	
Passeriformes	Tyrannidae	Tyrannus albogularis		Х	
Passeriformes	Tyrannidae	Tyrannus melancholicus		Х	х
Passeriformes	Tyrannidae	Conopias trivirgatus	х	х	х
Passeriformes	Tyrannidae	Lathrotriccus euleri	х	х	х
Passeriformes	Vireonidae	Cyclarhis gujanensis	х	х	х
Passeriformes	Vireonidae	Hylophilus semicinereus	х	х	х
Passeriformes	Vireonidae	Hylophilus brunneiceps	х	х	х
Passeriformes	Hirundinidae	Pygochelidon melanoleuca		х	
Passeriformes	Hirundinidae	Progne tapera	х	х	х
Passeriformes	Hirundinidae	Progne chalybea		х	
Passeriformes	Hirundinidae	Tachycineta albiventer		х	
Passeriformes	Hirundinidae	Hirundo rustica		х	
Passeriformes	Troglodytidae	Troglodytes musculus		х	
Passeriformes	Troglodytidae	Cantorchilus leucotis	x	х	
Passeriformes	Polioptilidae	Polioptila plumbea	х	х	х

Passeriformes	Polioptilidae	Polioptila facilis		х	
Passeriformes	Turdidae	Turdus leucomelas		х	x
Passeriformes	Turdidae	Turdus fumigatus	х	х	
Passeriformes	Turdidae	Turdus albicollis	Х	х	
Passeriformes	Fringillidae	Euphonia chrysopasta	Х	х	
Passeriformes	Passerellidae	Ammodramus aurifrons		х	
Passeriformes	Passerellidae	Arremon taciturnus	Х	х	Х
Passeriformes	Icteridae	Leistes militaris		x	
Passeriformes	Icteridae	Psarocolius decumanus	x	x	
Passeriformes	Icteridae	Cacicus cela	x	x	x
Passeriformes	Icteridae	Cacicus haemorrhous	x		
Passeriformes	Icteridae	lcterus croconotus		x	
Passeriformes	Thraupidae	Coereba flaveola	x	x	x
Passeriformes	Thraupidae	Volatinia jacarina		х	Х
Passeriformes	Thraupidae	Loriotus luctuosus		х	
Passeriformes	Thraupidae	Ramphocelus carbo		х	х
Passeriformes	Thraupidae	Sporophila americana		x	
Passeriformes	Thraupidae	Sporophila angolensis		x	x
Passeriformes	Thraupidae	Sicalis columbiana		x	
Passeriformes	Thraupidae	Paroaria gularis			x
Passeriformes	Thraupidae	Thraupis episcopus		x	
Passeriformes	Thraupidae	Thraupis palmarum		х	
Passeriformes	Thraupidae	Tangara mexicana		х	
Passeriformes	Thraupidae	Tangara velia		Х	
Total			118	163	107
Exclusive species			16	46	6







Figure S2. Distribution of bird species recorded<br/>in 57 sites of seasonally flooded forest by<br/>blackwater rivers (igapó) in the Negro River<br/>basin, Northwest Brazilian Amazon in relation to<br/>canopy closure. The species columns represent<br/>the presence of the species in each sampling<br/>site. The horizontal order of the top bar is based<br/>on the canopy closure gradient – from greater to<br/>lesser openness. The vertical order of the<br/>species was based on the number of sites where<br/>the species was recorded along the canopy<br/>closure gradient.

Ordered plots

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**Figure S3**. Relationships between bird species richness and canopy closure in treatment of seasonally flooded forest by blackwater rivers (igapó) with recent burns (2013 to 2022) in the Negro River basin, Northwest Brazilian Amazon. Gray areas around the linear trend lines represent 95% confidence intervals.

# CONCLUSÃO

Apresentamos dados sobre o efeito do fogo em comunidades de aves em florestas de igapó na bacia do Rio Negro, no noroeste da Amazônia. Investigamos como a composição e riqueza de espécies avifaunísticas respondem a incêndios em diferentes intervalos de tempo no passado. Nossos resultados mostram que o fogo modifica a estrutura da vegetação afetando consequentemente a comunidade de aves. A riqueza de espécies mostrou ser maior em igapós queimados recentemente, onde a abertura do dossel também foi maior. Todas as categorias de igapó mostraramse com composição de especies de aves diferentes, com a substituição de especies sendo a principal agente. Com os nossos resultados é possível perceber que mesmo após 38 anos do evento do fogo, a composição de aves não torna-se mais semelhante ao igapó não afetado. Esse achado é importante pois ressalta a necessidade da preservação das florestas alagadas, afim de promover a sobrevivência de espécies dependentes desse ambiente. Nossos resultados contribuem para a compreensão dos efeitos do fogo em comunidades de aves e dão aporte para que medidas de mitigação sejam estratégicas e levem em consideração o conjunto de organismos dependentes desse ambiente.

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PROGRAMA DE PÔS-GRADUAÇÃO EM ECOLOGIA

ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 19 dias do mês de Fevereiro do ano de 2024, às 14:h00min, via videoconferência, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: a Dr<sup>a</sup>. Maria Teresa Fernandez Piedade, do Instituto Nacional de Pesquisas da Amazônia – INPA, o Dr. Sérgio Henrique Borges, da Universidade Federal do Amazonas – UFAM e a Dr<sup>a</sup>. Camila Duarte Ritter, do Instituto Nacional de Pesquisas da Amazônia – INPA, sendo os suplentes o Dr. Flávio Kulaif Ubaid, da Universidade Estadual do Maranhão – UEMA e o Dr. Thiago Orsi Laranjeiras, do Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio, sob a presidência da orientadora, a fim de proceder a arguição pública do trabalho de DISSERTAÇÃO DE MESTRADO de CLEITON VALENTIM, intitulado: "EFEITO DO FOGO NA COMPOSIÇÃO DAS COMUNIDADES DE AVES EM ÁREAS ALAGÁVEIS NA BACIA DO RIO NEGRO", orientado pela Dr<sup>a</sup>. Camila Cherem Ribas, do Instituto Nacional de Pesquisas da Amazônia – INPA e João Marcos Guimarães Capurucho, da Universidade Pesquisas da Amazônia – INPA e João Marcos Guimarães Capurucho, da Universidade Pesquisas da Amazônia – UFA e João Marcos Guimarães Capurucho, da Universidade Pesquisa de Federal do puzel Dra.

Após a exposição, o(a) discente foi arguido oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

 X
 APROVADO (A)
 REPROVADO (A)

 X
 POR UNANIMIDADE
 POR MAIORIA

Nada mais havendo, a presente ata foi lida, lavrada e assinada pelos membros da Comissão Examinadora.

- DR<sup>a</sup>. MARIA TERESA FERNANDEZ PIEDADE
- DR. SÉRGIO HENRIQUE BORGES

DR<sup>a</sup>. CAMILA DUARTE RITTER

DR. FLÁVIO KULAIF UBAID

DR. THIAGO ORSI LARANJEIRAS

DA

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