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DINÂMICA DAS AVES AO LONGO DAS BORDAS ENTRE SAVANAS E FLORESTAS DE GALERIA EM UMA PAISAGEM DE SAVANA NEOTROPICAL

MACAPÁ, AP
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Dinâmica das aves ao longo das bordas entre savanas e florestas de galeria em uma paisagem de savana neotropical

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.

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"***O sucesso nasce do querer, da determinação e persistência em se chegar a um objetivo. Mesmo não atingindo o alvo, quem busca e vence obstáculos, no mínimo fará coisas admiráveis*"**.**

Nunca desistir – José de Alencar.

RESUMO

Sousa, Jackson Cleiton. Dinâmica das aves ao longo das bordas entre savanas e florestas de galeria em uma paisagem de savana neotropical. Macapá, 2020. Dissertação (Mestre em Biodiversidade Tropical) – Programa de Pós-graduação em Biodiversidade Tropical – Pró-Reitoria de Pesquisa e Pós-Graduação - Universidade Federal do Amapá.

Movimentos de espécies entre manchas de diferentes ecossistemas locais dentro de uma paisagem são denominados transbordamentos entre habitats. Estudamos as aves para entender os padrões gerais da movimentação das espécies entre savanas e florestas de galerias em uma paisagem de savana neotropical. Mais especificamente, avaliamos: (1) se as características ecológicas podem prever a probabilidade de uma espécie de ave cruzar uma borda ecológica; (2) a distância que uma espécie que vive na floresta-savana consegue se deslocar em um ambiente de savana; e (3) se a riqueza de espécies e a abundância total das espécies de aves de floresta-savana são influenciadas negativamente pela da distância à borda da floresta e positivamente pela estrutura da vegetação na savana. Contamos as aves e medimos a estrutura da vegetação ao longo de 17 transectos de 400 m perpendiculares às florestas de galeria em uma paisagem de savana neotropical no estado do Amapá, na Amazônia brasileira. Descobrimos que 57% das 153 espécies registradas em nossa área de estudo se movem entre florestas de galeria e savanas. A propensão de uma espécie de se mover além das bordas é positivamente influenciada pela abundância das espécies e estrato de forrageamento, mas não pela massa corporal ou nível trófico. As espécies de floresta-savana movem-se, em média, 71,6 m da borda da floresta para a savana. Finalmente, a riqueza de espécies e a abundância total de espécies de floresta-savana diminuem com o aumento da distância da borda da floresta em direção a matriz savana e aumentam com a altura média das árvores e arbustos. Estes três resultados sugerem que os movimentos ao longo das bordas entre as florestas de galeria e as savanas são muito mais intensos do que se pensava anteriormente, são bidirecionais e devem ser levados em consideração ao elaborar estratégias de conservação para regiões de savana neotropical.

Palavras-chave: movimento; ecologia; amazônia; cruzamentos; paisagem;

ABSTRACT

Sousa, Jackson Cleiton. Bird dynamics along forest-savanna boundaries in a neotropical savanna landscape. Macapá, 2020. Dissertation (Master in Tropical Biodiversity) – Graduate Program in Tropical Biodiversity - Federal University of Amapá.

Movements of species between patches of different local ecosystems within a landscape are termed “cross-habitat spillovers.” We studied birds to understand the general patterns of cross-habitat spillovers between gallery forests and savannas in a neotropical savanna landscape. More specifically, we assessed: (1) if ecological traits can predict the likelihood of a bird species crossing an ecological boundary; (2) how far from the boundary a spillover species can move into the savanna; and (3) if the species richness and total abundance of spillover bird species are negatively influenced by the distance from the boundary and positively influenced by the vegetation structure. We counted birds and measured the vegetation structure along 17 400-m transects perpendicular to gallery forests in a neotropical savanna landscape in the state of Amapá in the Brazilian Amazon. We found that 57% of the 153 species recorded in our study area move between gallery forests and savannas. The propensity of a species to move across boundaries is positively influenced by abundance and foraging stratum, but not by body mass or trophic level. Spillover species move, on average, 71.6 m from the boundary into the savanna. Finally, the species richness and total abundance of spillover species decrease with the distance from the boundary and increase with the mean tree height. These three findings suggest that the cross-habitat movements along the boundaries between gallery forests and savannas are much more intense than previously thought, are bidirectional, and should be taken into account when designing conservation strategies for neotropical savanna regions.

Keywords: movement; ecology; Amazon; spillovers; landscape.

SUMÁRIO

1. INTRODUÇÃO GERAL

As savanas neotropicais formam um dos ambientes mais heterogêneos da América do Sul e cobrem uma área com cerca de 2 milhões de km² distribuídas de forma disjunta pelo continente (Silva and Bates 2002). Em geral, as paisagens das savanas neotropicais são compostas por uma matriz de vegetação aberta e semiaberta que varia em sua fisionomia e composição (Ribeiro and Walter 1998), sendo conhecidas cinco principais fitofisionomias: o *cerradão* (um tipo de floresta densa (8 a 15 m de altura) que geralmente possui um dossel completamente fechado), o *cerrado sensu stricto* (uma floresta (5 a 8 m de altura) com mata fechada e mais árvores dispersas do que no cerradão), o *campo cerrado* (uma mata aberta (3-6 m de altura) com poucas árvores), o *campo sujo* (pastagem (2-3 m de altura) com arbustos dispersos) e o *campo limpo* (prados com poucos ou nenhum arbusto ou plantas lenhosas mais altas) (Eiten 1972, Ribeiro and Walter 1998).

As paisagens das savanas neotropicais também podem ser intercaladas por fisionomias florestais e de alagados, como as *florestas de galeria* que formam dossel contínuo (com árvores com altura ~ 25 m) que ocorrem como faixas relativamente estreitas (em média 200 m de largura) ao longo dos cursos de água (Eiten 1972, Ribeiro and Walter 1998, Silva and Bates 2002, Zhang et al. 2019), além das *veredas* que são formadas por cinturões de palmeiras (exemplo *Mauritia flexuosa*, *Euterpe oleracea* e *Mauritiella aculeata*) nos vales estreitos, e dos *campos sazonalmente inundados* (Silva et al. 1997, Ribeiro and Walter 1998, Costa-Neto et al. 2017).

As duas maiores regiões de savana na América do Sul estão no Planalto Central do Brasil (conhecido como Bioma Cerrado) que inclui também partes da Bolívia e Paraguai, e nos Llanos na Venezuela e Colômbia (Ribeiro and Walter 1998, Silva and Bates 2002, Carvalho and Mustin 2017, Stier et al. 2020). Entretanto, pequenas manchas de savanas podem ser encontradas isoladas dentro do bioma Amazônia, sendo conhecidas como “savanas amazônicas” (Ribeiro and Walter 1998, Carvalho and Mustin 2017, Stier et al. 2020). As savanas amazônicas cobrem aproximadamente 267.164 km², das quais cerca de 150.000 km² estão presentes Amazônia brasileira (Carvalho and Mustin 2017) localizadas no norte dos estados do Pará (ilha do Marajó, região do Alto Parú, região de Monte Alegre, região do rio Trombetas, Santarém, Serra dos Carajás e Serra do Cachimbo), Amazonas (Humaitá), Roraima (complexo Roraima-Rupununi) e Amapá (faixa longitudinal de norte-sul, paralela à costa atlântica) (Pires and Prance 1985, Barbosa et al. 1997, Ribeiro and Walter 1998, Daly and

Mitchell 2000, Silva and Bates 2002, Aleixo and Poletto 2007, Carvalho and Mustin 2017, Mustin et al. 2017). Alguns estudos revelam que as savanas amazônicas atuais possivelmente possuíam conexões com as demais savanas de fora da Amazônia, e suas formações ocorreram por eventos de expansão e retração das florestas úmidas e secas durante os ciclos climáticos quaternários, da qual as florestas secas e as formações vegetais abertas (campos e savanas) se expandiram em algumas regiões da Amazônia, enquanto as florestas tropicais se retraíram para as regiões mais úmidas (Silva et al. 1997, Silva and Bates 2002, Costa-Neto 2014). Todos esses eventos paleo-climáticas associadas às mudanças vegetacionais foram consideradas como um dos fatores que levaram à especiação de organismos florestais e savânicos na América do Sul (Silva et al. 1997, Silva and Bates 2002, Vasconcelos et al. 2011).

Assim como a Floresta Amazônica, as savanas neotropicais são bastantes conhecidas por abrigarem uma vida selvagem exuberante, sendo inclusive ambiente rota de passagem para muitas espécies de aves migrantes (por exemplo alguns Charadriiformes, Passeriformes, Falconiformes, etc.) (Silva 1995, Silva and Bates 2002, Santos and Silva 2007). Vários trabalhos foram publicados descrevendo a fauna e flora nas savanas neotropicais da América do Sul, sendo conhecidas 10.000 espécies de plantas, 161 espécies de mamíferos, 856 espécies de aves, 120 espécies de répteis e 150 espécies de anfíbios (Haverschmidt and Mess 1994, Silva 1995, Ratter et al. 1997, Silva et al. 1997, Mees 2000, Sanaiotti and Cintra 2001, Ratter et al. 2001, 2003, Bridgewater et al. 2004, Tubelis et al. 2004, Klink and Machado 2005, Silva and Santos 2005, Aleixo and Poletto 2007, Santos and Silva 2007, Boss 2009, Tubelis 2009, Aguiar and Naiff 2010, Schunck et al. 2011, Vasconcelos et al. 2011, Silva et al. 2013, Ribeiro 2014, Costa-Neto 2014, Boss and Silva 2015, Godoi et al. 2016, Costa-Neto et al. 2017, Carvalho et al. 2018), e várias espécies de muitos grupos sendo consideradas endêmicas (Rizzini 1979, Silva 1997, Myers et al. 2000, Silva and Bates 2002, Ribeiro et al. 2016, Mustin et al. 2017, Stier et al. 2020).

Esta rica biodiversidade está em perigo, pois nas últimas décadas, as regiões de savanas neotropicais, principalmente as savanas amazônicas, foram tiveram suas áreas naturais transformadas em áreas de agricultura comercial, monocultura e de pastejo, restando poucas áreas com vegetação nativa (Silva and Bates 2002, Klink and Moreira 2002, Mittermeier et al. 2011), e as projeções mostram que as savanas serão uma das regiões mais afetados negativamente pelas mudanças climáticas (Torres and Marengo 2014, Silva et al. 2019, Grande et al. 2020).

Os critérios usados para a conservação dos ecossistemas não-florestais na Amazônia diferem daqueles usados para os ecossistemas florestais. Por exemplo, para os ecossistemas não-florestais, como as savanas, a legislação exige a proteção de 35% da vegetação em reserva legal. Por outro lado, a exigência para os ecossistemas florestais é de 80%. Além disso, há acordos, decretos e leis que são aplicados somente para garantir a conservação dos ambientes florestais na Amazônia, mas que não valem para os não-florestais (Overbeck et al. 2015, Carvalho et al. 2019). Por isso, é importante intensificar os estudos ecológicos sobre a biota das savanas para propor medidas mitigadoras que visem a conservação da sua biodiversidade (Silva and Bates 2002, Tubelis et al. 2004, Ribeiro 2014, Ribeiro et al. 2016, Carvalho and Mustin 2017, Mustin et al 2017, Hilário et al. 2017, Silva and Barbosa 2018).

Estratégias de conservação sólidas requerem um bom conhecimento sobre como os organismos se distribuem no tempo e no espaço (Silva and Bates 2002). Em paisagens heterogêneas, os organismos podem se deslocar entre manchas de um ecossistema local com a mesma fitofisionomia, com fitofisionomias diferentes ou entre manchas de diferentes ecossistemas locais. As espécies que fazem estes movimentos atravessando as bordas de diferentes habitats, são conhecidas como espécies “spillover” (Blitzer et al. 2012). Espécies “spillover” podem se movimentar entre habitats pela escassez ou disponibilidade sazonal de recurso alimentar (como frutas, flores, sementes e insetos), pela procura de materiais para construção de ninhos (como galhos, gravetos, musgos, capins, etc.) ou por alterações antrópicas nos habitats (Dunning et al. 1992, Tubelis et al. 2004, Boss and Silva 2015).

O movimento de espécies entre habitats resultam da probabilidade dos organismos encontrarem a borda (o limite) de um habitat e sua capacidade de atravessar a borda para o outro habitat (Wiens 1992). Se uma mancha de habitat é pequena ou estreita, com alta razão perímetro:área, a probabilidade de um organismo encontrar sua borda é alta, caso contrário, a probabilidade é baixa. Ao se deparar com uma borda, a probabilidade de um organismo atravessá-la também depende da permeabilidade da borda, que pode ser definida como o grau pelo qual uma borda restringe os movimentos de uma espécie (Wiens et al. 1985).

A permeabilidade da borda, é uma função da própria borda e das características do organismo. Assim, se dois habitats adjacentes são muito diferentes em suas fisionomias, a borda entre eles tem alto contraste. Consequentemente, se a diferença entre habitats não for pronunciada, a borda terá baixo contraste (Ewers and Didham 2006, Biswas and Wagner 2012, Hou and Walz 2016). Estas variações de alto e baixo contraste entre os dois habitats estão relacionadas às diferenças na estrutura da vegetação (por exemplo densidades de árvores e arbustos, altura de árvores e cobertura do dossel, etc.), composição florística, microclima e outras características ecológicas (Furley and Ratter 1988, Jayapal et al. 2009, Jankowski et al. 2012, Bueno et al. 2018), e como os organismos podem perceber as bordas de diferentes maneiras, suas características ecológicas (como estrato de forrageamento, grupo trófico e peso) ou espécies mais abundantes, podem predizer como eles responderão a uma borda (Ewers and Didham 2006, Lees and Peres 2009). Finalmente, se a borda for ultrapassada, os organismos podem se mover a diferentes distâncias para o habitat adjacente, seja ele suplementar (contenha recursos adicionais ou substituíveis) ou complementar (compartilhamento dos recursos entre si) (Dunning et al. 1992). Em geral, os modelos simples de difusão preveem que a maioria dos organismos não se afastam muito das bordas e que apenas alguns poucos alcançam longas distâncias (Wiens 1992). Se essa previsão estiver correta, também é esperado que a riqueza total de espécies e a abundância total desse grupo de espécies “spillover” diminuam com a distância da borda (Tubelis et al. 2004). Os movimentos das espécies entre habitats são importantes, pois eles influenciam vários processos ecológicos tais como dispersão de sementes que, por sua vez, podem influenciar a sucessão vegetal e assim influenciar a composição e a configuração dos ecossistemas locais (Wiens et al. 1985, Silva et al. 1996).

A maioria dos estudos sobre movimentos entre habitats em ambientes tropicais foi realizada entre ecossistemas naturais (geralmente florestas) e ambientes formados pelo homem (por exemplo áreas de agricultura) (Silva et al. 1996, Boesing et al. 2018), com alguns investigando os movimentos entre habitats entre ecossistemas naturais (Tubelis et al. 2004). Um laboratório natural para estudos sobre movimentos entre habitats e entre ecossistemas naturais são as savanas neotropicais. As bordas entre florestas de galeria e as áreas abertas e semiabertas das savanas têm alto contraste, portanto, o esperado seria que os movimentos de espécies entre esses dois tipos de ecossistemas locais fossem limitados (Wiens 1992). No entanto, estudos mostram que várias espécies de vertebrados (por exemplo morcegos, mamíferos terrestres e aves) encontrados em regiões de savana neotropical usam florestas e savanas (Silva 1995, Mittermeier et al. 2010, Vasconcelos et al. 2011, Boss and Silva 2015, Carvalho et al. 2018, Piña et al. 2019), sugerindo um intenso movimento através das bordas desses dois ecossistemas (Silva 1995). Além disso, há evidências de que o cruzamento das bordas entre florestas de galeria e savanas não é unidirecional, já que espécies de vertebrados que habitam mais as florestas de galeria foram relatadas usando savanas (Johnson et al. 1999, Tubelis et al. 2004) e espécies de vertebrados que habitam as savanas, foram relatadas usando florestas de galeria (Redford and Fonseca 1986, Cavalcanti 1992, Boss and Silva 2015).

Neste sentido, esta dissertação teve como objetivo principal entender os padrões gerais da movimentação das aves entre savanas e florestas de galeria (chamadas aqui de aves de florestas-savanas) em uma paisagem de savana neotropical, bem como para estimar a quantidade de habitat necessária para manter os processos ecológicos nos quais estas espécies fazem parte. As aves foram escolhidas como modelo de táxon por serem diversas, mais conhecidas dentre os estudos faunísticos nas savanas neotropicais, além de serem relativamente fáceis de identificar, poder acessar recursos espacialmente dispersos e desempenhar um papel importante em várias funções ecológicas (como sendo agentes polinizadores, dispersores de sementes, controladores das populações de insetos, etc) (Sick 1997, Bibby et al. 2000, Levey et al. 2005, Sekercioglu et al. 2016) e serem utilizadas como bioindicadores ambientais (Oren 2001, Antas and Almeida 2002, Piratelli et al. 2008). Mais especificamente foi avaliado: (1) se as características ecológicas (grupo trófico, estrato de forrageamento e massa corporal) e abundância total predizem a probabilidade de uma espécie atravessar uma borda ecológica (Ewers and Didham 2006, Lees and Peres 2009), (2) se poucas espécies de floresta-savana serão capazes de se afastarem das bordas para o interior da savana (Wiens 1992) e por fim, (3) se a riqueza total de espécies e a abundância total de espécies de aves de floresta-savana são influenciadas negativamente pela distância da borda da floresta de galeria e positivamente pela estrutura da vegetação (densidade e altura de árvores e arbustos) da matriz savana (Tubelis et al. 2004). Essas informações podem ser importantes na tomada de decisões para subsidiar políticas de manejo e conservação de áreas mínimas de savana ao longo das florestas de galeria nas savanas neotropicais para que possam manter sua biodiversidade e seus processos ecológicos, tendo em vista que os habitats não-florestais, como por exemplo as savanas, não possuem a mesma proteção do que os ecossistemas florestais (Brasil 2012).

2. HIPÓTESES

- As características ecológicas (grupo trófico, estrato de forrageamento e peso) predizem a probabilidade de uma espécie de ave cruzar a bordas entre florestas de galeria e savanas (Ewers and Didham 2006);

- As espécies mais abundantes são mais capazes de cruzar as bordas entre florestas de galeria e savanas do que espécies menos abundantes (Lees and Peres 2009);

- Poucas espécies de aves de floresta-savana se afastam das bordas, sendo que a maioria delas não se deslocam em média acima de 60 m (Wiens 1992, Tubelis et al. 2004);

- A riqueza e a abundância total de espécies de aves de floresta-savana são influenciadas negativamente pelo aumento da distância à borda da floresta de galeria e positivamente pelas densidade e altura das árvores e arbustos da vegetação da savana (Tubelis et al. 2004).

3. OBJETIVOS

3.1 Geral

Estudar a dinâmica de movimentação das aves entre as bordas de florestas de galeria e savanas em uma paisagem de savana amazônica no estado do Amapá, Brasil.

3.2 Específicos

- Estimar a riqueza e abundância de aves ao longo das bordas entre florestas de galeria e savana;

- Relacionar as espécies com base nos três grupos: (a) espécies florestais (exclusivas da floresta), (b) espécies de savana (exclusivas da matriz savana) e (c) espécies de floresta-savana (que deslocam-se entre floresta e matriz savana);

- Definir as características ecológicas (grupo trófico, estrato de forrageamento, peso) das espécies de aves de floresta-savana;

- Verificar a variação da estrutura da vegetação (densidade e altura das árvores e arbustos) ao longo das bordas entre florestas de galeria e matriz savana;

- Analisar as distâncias que as aves de floresta-savana se afastam da borda da floresta de galeria em direção à matriz savana;

- Avaliar a influência do aumento da distância da borda da floresta de galeria e da densidade e altura das árvores e arbustos da matriz savana sobre a riqueza e abundância total de aves de floresta-savana.

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ARTIGO CIENTÍFICO

Bird dynamics along forest-savanna boundaries in a neotropical savanna landscape

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Bird dynamics along forest-savanna boundaries in a neotropical savanna landscape

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Abstract

Movements of species between patches of different local ecosystems within a landscape are termed “cross-habitat spillovers.” We studied birds to understand the general patterns of cross-habitat spillovers between gallery forests and savannas in a neotropical savanna landscape. More specifically, we assessed: (1) if ecological traits can predict the likelihood of a bird species crossing an ecological boundary; (2) how far from the boundary a spillover species can move into the savanna; and (3) if the species richness and total abundance of spillover bird species are negatively influenced by the distance from the boundary and positively influenced by the vegetation structure. We counted birds and measured the vegetation structure along 17 400-m transects perpendicular to gallery forests in a neotropical savanna landscape in the state of Amapá in the Brazilian Amazon. We found that 57% of the 153 species recorded in our study area move between gallery forests and savannas. The propensity of a species to move across boundaries is positively influenced by abundance and foraging stratum, but not by body mass or trophic level. Spillover species move, on average, 71.6 m from the boundary into the savanna. Finally, the species richness and total abundance of spillover species decrease with the distance from the boundary and increase with the mean tree height. These three findings suggest that the cross-habitat movements along the boundaries between gallery forests and savannas are much more intense than previously thought, are bidirectional, and should be taken into account when designing conservation strategies for neotropical savanna regions.

Keywords: movement, ecology, Amazon, spillovers, landscape

Introduction

Landscapes are mosaics of local ecosystems distributed among an area ranging from 1 km2 to 10,000 km2 [1]. In landscapes, mobile species move within local ecosystems, whether it is between patches of the same or different local ecosystem type.s. Species moving between patches of different local ecosystems are cross-habitat spillovers [2]. Cross-habitat spillovers can influence ecosystem processes such as succession, and thus change the location, composition, and structure of local ecosystems [3,4]. Therefore, a thorough understanding of the major patterns of cross-habitat movements is required to design conservation systems that aim to maintain viable populations of as many wild species as possible, keep ecological flows, and enable the resilience of ecosystems against the effects of global changes [5].

Cross-habitat movements are a consequence of the probability that organisms encounter a boundary between local ecosystems and that, once met, it will be crossed [6]. If a habitat patch is small or narrow, with a high perimeter-area ratio, the probability that an organism encounters its boundary is high; otherwise, the probability is low. When facing a boundary, the likelihood of an organism to cross it depends on the permeability of the boundary, which can be defined as the degree by which a boundary constrains the movements of a species [3]. The boundary permeability, in turn, is a function of the boundary itself and the characteristics of the organism. Thus, if two adjacent ecosystems are very different in their physiognomies, their boundary has high contrast. Accordingly, if the difference between ecosystems is not pronounced, their boundary has low contrast. Because organisms can perceive boundaries in different ways, their ecological traits, such as trophic level, body size, and abundance, can predict how they respond to an ecological boundary [7]. Furthermore, if a boundary is crossed, organisms can move into the adjacent ecosystem over different distances. In general, simple diffusion models predict that most of the organisms do not move very far from the boundary, and that only a few reach long distances [6]. If this prediction is right, the total species richness and total abundance of spillover species are expected to decline with the distance from the boundary [8,9].

Most studies on cross-habitat movements in tropical environments were carried out between natural (usually forests) and human-made ecosystems [4,10], with few investigating cross-habitat movements between natural ecosystems [10]. Neotropical savanna regions are a natural laboratory for studies on cross-habitat spillovers between natural ecosystems. These regions are dominated by landscapes composed by a matrix of open and semi-open vegetations that are intersected by tall (up to 25 m), evergreen gallery forests that occur as relatively narrow strips (no more than 200 m in width) along watercourses [11]. Because the boundaries between gallery forests and savannas have high contrast, movements of species between these two types of local ecosystems are expected to be limited [11]. However, biogeographic studies show that several terrestrial vertebrate species found in neotropical savanna regions use both forest and savannas, suggesting an intense movement across these two ecosystems [12]. Moreover, there is evidence that boundary-crossing between gallery forests and savannas is not unidirectional, as vertebrate species living in gallery forests were reported using savannas [e.g., 9,13] and savanna vertebrate species were reported using gallery forests [e.g., 14,15].

Understanding the biological dynamics along the boundaries between gallery forests and savannas is important to guide conservation policies for neotropical savannas. These landscapes are among the world’s most threatened ecoregions due to the accelerated expansion of large-scale commercial agriculture [11,16,17] and climate change [18–20]. Although some countries have safeguards to protect gallery forests due to their importance in maintaining water resources, most of these safeguards ignore the role played by adjacent savannas in supplementing or complementing the resources required by gallery forests' species to survive [19,20].

Here, we studied birds to understand the general patterns of cross-habitat spillovers between gallery forests and savannas in a neotropical savanna landscape, as well as to estimate the amount of habitat required to maintain these ecological processes. Birds were chosen as model taxon for this study because they are diverse, well-known, relatively easy to identify, can access spatially dispersed resources, and play an important role in several ecological functions [21,22]. More specifically, we assessed: (1) if ecological traits (trophic group, foraging stratum, body mass [in grams], and total abundance) can predict the likelihood of a bird species crossing an ecological boundary; (2) how far from the boundary a spillover species can move into the savanna; and (3) if the species richness and total abundance of spillover bird species are negatively influenced by the distance from the boundary and positively influenced by the vegetation structure [21,22].

Methods

Study region

We carried out our study in the savanna region in the State of Amapá of the Brazilian Amazon (Fig 1). This region is a narrow longitudinal strip parallel to the Atlantic coast, occupying an area of approximately 10,021 km^2 [23,24] The Amapá savannas are dominated by upland savannas that are intersected by gallery forests and seasonally flooded grasslands along the rivers [25]. The upland savanna has a grass layer that includes species of *Rhynchospora*, *Axonopus*, *Paspalum*, *Polygala*, *Bulbostylis* and *Miconia*, and a woody layer that includes large shrubs and trees from 3 to 10 m, such as *Byrsonina crassifolia*, *Salvertia convallariodora*, *Ouratea hexasperma*, *Curatella americana*, *Himatanthus articulatus*, *Pallicourea rigida,* and *Hancornia speciosa* [26,27]. Gallery forests are, on average, narrow (~ 300 m) and found in hydromorphic soils rich in organic matter, along narrow perennial streams that occur across the region [25]. They are evergreen, with an understory dominated by housing ferns, epiphytes, and palm trees. The forest canopy is dominated by tall trees from 15 to 30 m, such as *Jacaranda copaia*, *Symphonia globulifera*, *Desmoncus* sp., *Annona paludosa*, *Coccoloba* sp, *Ficus* sp., *Virola* sp., *Lecythis* sp. and *Hymenaea parvifolia* [27]. Seasonally flooded grasslands are found in narrow valleys, where the soils are shallow and permanently flooded. These grasslands sometimes have belts of palm species, such as *Mauritia flexuosa*, *Euterpe oleracea,* and *Mauritiella aculeata* [25,27]. The climate of the Amapá savanna regionis hot (~ 27ºC) and humid (average relative humidity of 81%), with high annual precipitation (2,700 mm) and a distinct dry season from August to November, a period of high temperature and water deficit due to reduced rainfall (~ 234.5 mm) [15].

Sample design

We selected 17 sites in a 70,000 hectare landscape (0º16'31"N, -51º04'05"W) that well represents the environmental variation found in the Amapá savannas (Fig 1). These sites were chosen according to three criteria: (1) they were at least 1.5 km apart to ensure spatial independence between them [21]; (2) forests and savannas were well-marked (with high contrast boundaries) without any gradual transition between them; and (3) gallery forests were separated from one another by at least 700 m to avoid detecting bird species that were moving between forests across the savannas. At each site, we set a 450 m linear transect perpendicular to the gallery forests. Each transect was marked at 50 m intervals (henceforth, “distance classes”) with colored ribbons nailed to tree trunks. The first interval was within the gallery forest, whereas the eight remaining intervals represented savannas at different distances from the boundary.

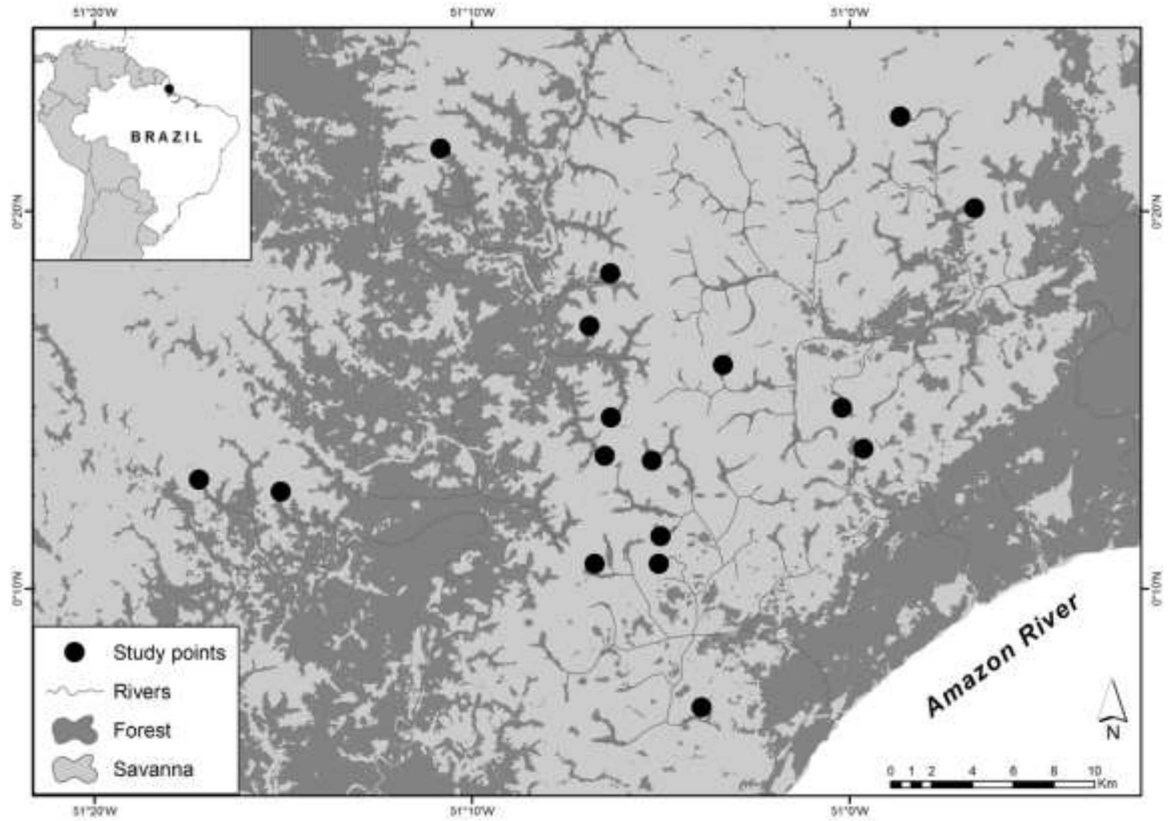

Fig 1. Study area in Amapá, Brazil. Dots represent the sites where birds and vegetation were surveyed.

Bird sampling and traits

To estimate bird species richness and bird species abundance across the transects, we used the fixed distance transect method, which consists of counting all birds detected visually or aurally within 50 m on each side of the transect [21]. Birds were counted four times from April to September 2019, twice during the rainy season (April and June), and twice during the dry season (July and September). Thus, our counts included all the critical periods of the region's annual bird cycle [e.g., 29,30]. We counted birds between 6:00 am and 10:30 am to maximize the detection of species [31]. Each transect was sampled for 90 minutes, at an average speed of 0.4 km/hour, and the direction from which the counting began (forest ↔ savannah) was chosen randomly one day before the sampling. We recorded the start and end times of each count, the identity of the recorded species (observed or heard), the number of individuals, and the distance interval from the forest. The counts were made by one of us (JC) with the aid of Olympus (7×32mm) and Bushnell (10×42mm) binoculars and a Canon PowerShot SX60 camera. The vocalizations, when necessary for the identification of the species, were recorded with a Sony recorder and directional microphone Yoga-Ht81. We gathered the information for four ecological traits for each bird species: (a) trophic group (herbivores, insectivores, carnivores, and omnivores), (b) foraging stratum (low-, mid-, high-stratum, and multiple-strata), (c) body mass (in grams), and (d) total abundance. The classification of species in trophic groups was based on our personal field experience with additional information from the literature [32]. The classification of the species' foraging height (ground, mid-level, upper-level, and multi-strata) was based on Stotz et al. [33] and our observations, while information on body mass was taken from Wilman et al. [7,32] The total number of records for each species during all four counts represents a species' abundance.

Vegetation structure

To characterize the structure of the vegetation along the transects, we counted and measured the heights of all trees and shrubs along a 2 m belt on one side of the transects. Then, we calculated the tree density (m^2) and the mean tree height (m) for each distance class (50 m intervals) along all transects. The trees' height was measured using a 4.5 m graduated ruler and a Bushnell Hypsometer (Scout 1000 Arc).

The laser was launched on the highest branches, branches, or leaves, and the hypsometer data was recorded. Then, a formula [sin (Angle × π / 180) * Distance from the object + 1.59 (eye height)] was used to obtain the height of each tree.

Data Analysis

We included all species recorded in the statistical analyses, except nocturnal species, vultures, ibises, ducks, and aerial insectivores, all of which were incompletely sampled. The distribution of species along the transects was used to classify them into three groups: (a) forest species (i.e., species recorded solely in gallery forests), (b) savanna species (i.e., species recorded only in savannas), and (c) spillover species (i.e., species found in both savanna and gallery forests). We used a probit regression to assess if ecological traits can predict a species' likelihood to cross a boundary. To determine how far, on average, a spillover species can move into the savanna, we took all its records within the savanna and calculated the average of the distances of these records to the boundary. To model the effects of distance from the forest, tree density, mean tree height, and season on the species richness and total species abundance of spillover species, negative binomial regressions considering the transects as a random factor were used. All statistical tests were made using Stata [7,34].

Results

We collected 2.007 records of 153 species of birds distributed in 33 families (S1 Table). Of these species, 88 were spillovers, as they were recorded in both savannas and gallery forests. 65 were non-spillover species, 11 were recorded solely in gallery forests, and 54 were found exclusively in the savannas. The probit regression was significant (Wald test = 21.02, df = 8, $p < 0.01$) and correctly classified 62.1% of the species in spillovers and no-spillovers (Table 1).

Some ecological traits influenced the propensity of a species to cross the boundary between gallery forest and savanna ecosystems. Abundance increased the likelihood of a species to cross a boundary (Table 1). Furthermore, species that forage in high-stratum were more likely to cross the boundary than species foraging on the ground (Table 1), but not more than species foraging in the mid-stratum (c^2 = 1.03, p = 0.30) or multiple strata (c^2 = 0.00, p = 0.97). Finally, body mass and the trophic group did not influence boundary-crossing (Table 1).

Table 1. Results of the binomial probit regression showing the relationship between no-spillover species (0) and spillover species (1) with four morpho-ecological traits.

Variables	Coefficient	Robust standard error	Z	P
Intercept	-0.846	0.414	-2.04	0.041
Trophic Group[a]				
Insectivore	0.079	0.294	0.27	0.787
Carnivore	-0.064	0.446	-0.14	0.885
Omnivore	-0.226	0.285	-0.79	0.427
Foraging Stratum[b]				
Mid-stratum	0.662	0.526	1.26	0.208
High stratum	1.081	0.402	2.68	0.007
Multiple strata	0.648	0.412	1.57	0.116
Body mass (g)	0.000	0.00	-0.16	0.877
Total Abundance	0.018	0.005	3.12	0.002

a. Compared to herbivore

b. Compared to ground

Spillover species can move from the boundary into the savannas over different distances (S2 Table). The average distances away from the boundary between galley forests and savannas over which spillover species were observed ranged from 25 to 225 m (mean = 71.6, SD = 49.2, n = 88). In general, most species (52.3%) did not move, on average, more than 60 m from the boundary. Nevertheless, several spillover species (23.8%) were recorded beyond 100 m (Fig 2).

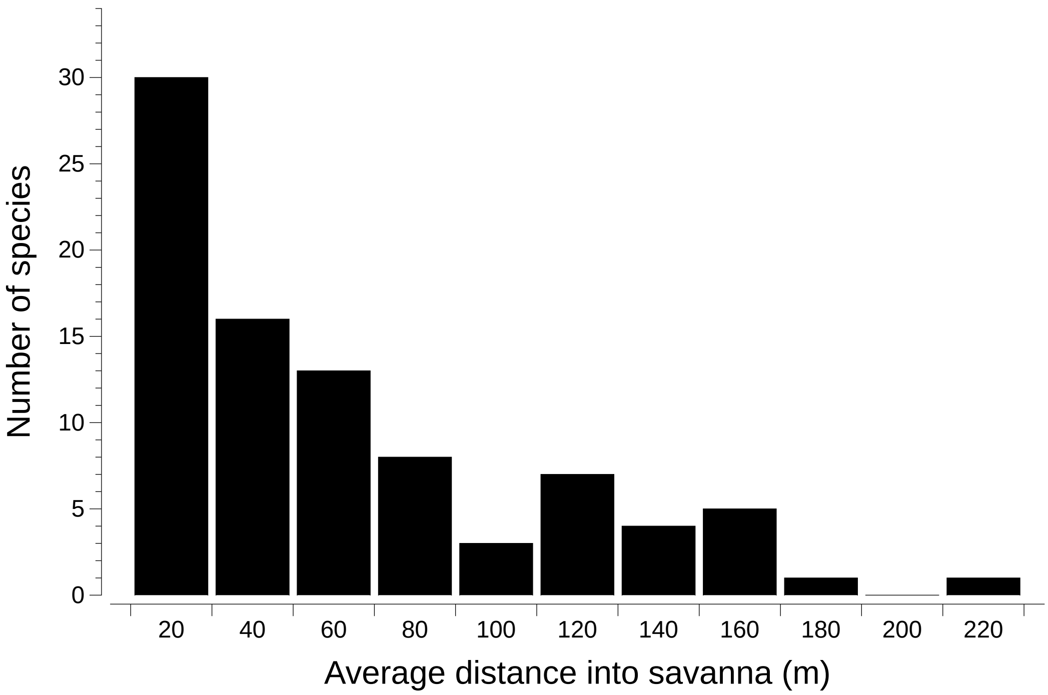

Fig 2. Average distances (in m) over which spillover species were observed from the boundary into the savanna in Amapá, Brazil.

The distance from the boundary and one indicator of habitat structure influenced species richness and total abundance of spillover species within the savanna matrix.

Both negative binomial regressions were significant (species richness: Wald test = 343.3, df = 5, $p < 0.001$; total abundance: Wald test = 193.04, df = 5, $p < 0.001$) and show that species richness and total abundance of spillover species declined with the distance from the forest (Fig 3), increased with the mean tree height (Fig 4), and were not influenced by tree density or season (Table 2).

Table 2. Results of the negative binomial regression showing the relationships between the richness and abundance of spillover species with the distance from the boundary and vegetation structure (mean tree height and tree density, in individuals/m^2).

Models	Coefficient	Robust standard error	z	P
Richness				
Intercept	0.543	0.269	2.02	0.004
Distance from forest	-0.008	0.001	-13.21	0.000
Tree density (m^2)	0.927	0.992	0.93	0.350
Mean tree height (m)	0.516	0.149	3.45	0.001
Season[a]	0.040	0.121	0.33	0.741
Abundance				
Intercept	0.678	0.272	2.50	0.013
Distance from forest	-0.007	0.001	-9.32	0.000
Tree density (m^2)	1.452	1.299	1.12	0.264
Mean tree height (m)	0.533	0.161	3.31	0.001
Season[a]	0.012	0.158	0.08	0.938

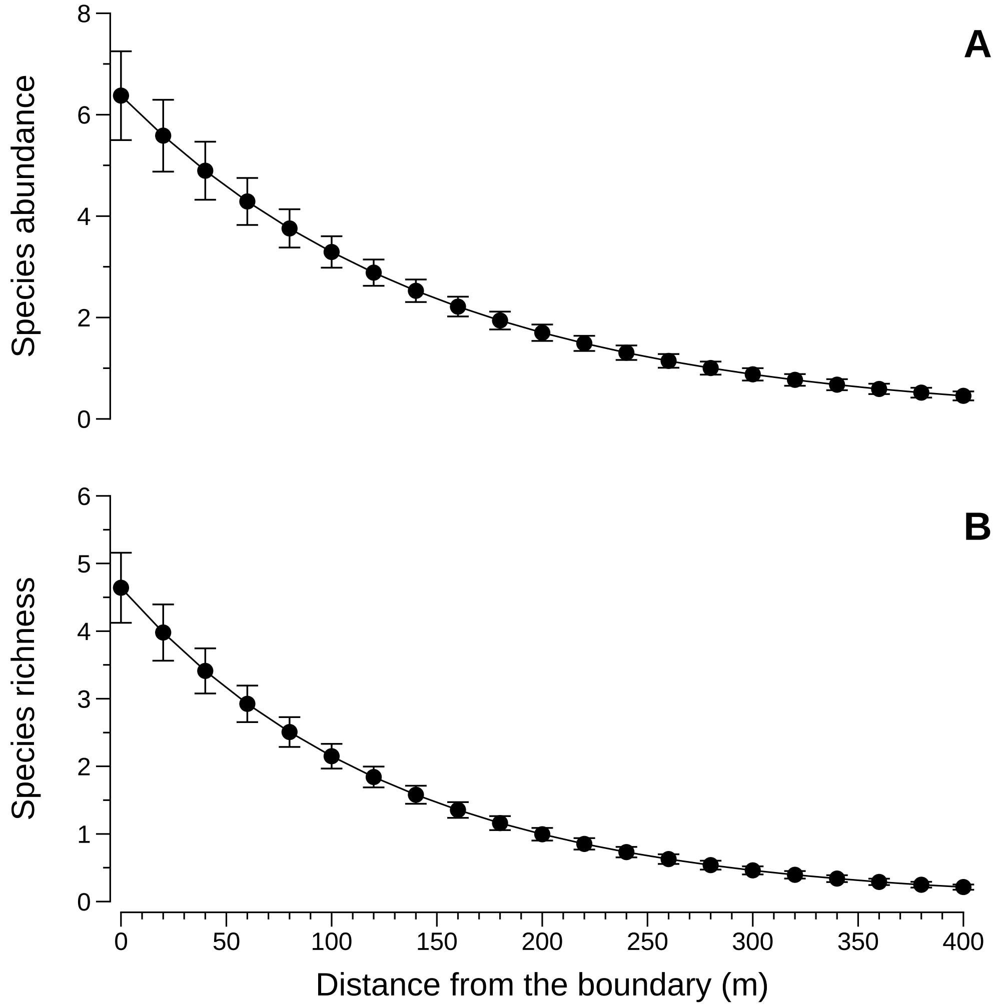

Fig 3. Predicted number of species richness (a) and abundance of spillover species (b) in relation to the distance of the boundary between gallery forest and savanna, when controlling for tree height and plant density in a savanna landscape in Amapá, Brazil.

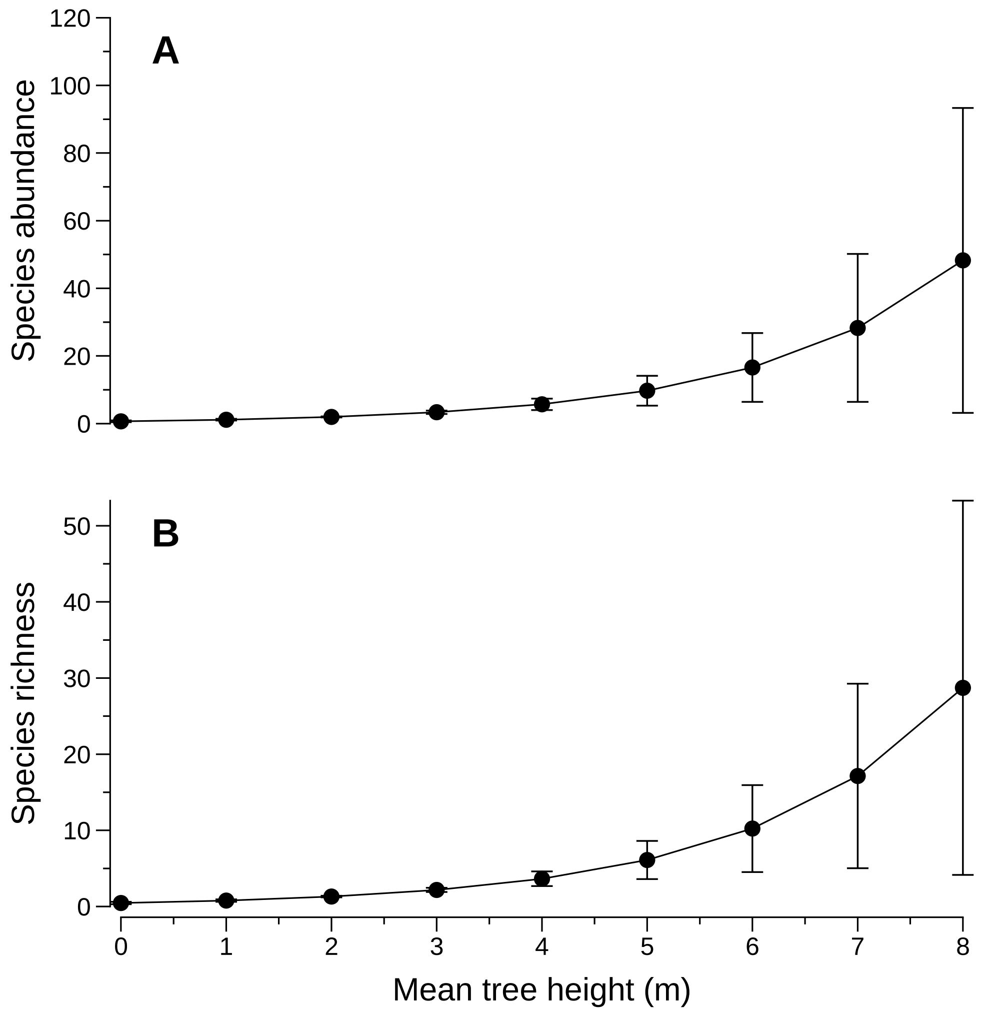

Fig 4. Predicted number of species richness (a) and abundance of spillover species (b) in relation to the mean tree height, when controlling plant density and distance from the boundary between gallery forest and savanna in a savanna landscape in Amapá, Brazil.

Discussion

We documented the cross-habitat movements between gallery forests and savannas by birds in a neotropical savanna landscape. Among the 153 species recorded, 57.5% used both gallery forests and savannas. Abundance positively influences the propensity of a species to move across boundaries. Moreover, we found that spillover species move, on average, up to 71.4 m from the boundary, but that several species can reach, on average, up to 225 m. Finally, the richness and the total abundance of spillover species decrease with the distance from the boundary and increase with the mean tree height. These three findings suggest that the cross-habitat movements along the boundaries between gallery forests and savannas are much more intense than previously thought, bidirectional, and should be considered when designing conservation strategies for neotropical savanna regions.

The fact that almost 88 species recorded in our study were able to cross the boundaries between gallery forests and savannas is surprising because the boundaries separating these two ecosystems have high contrast, and the two ecosystems are very different in structure, floristic composition, microclimate, and other ecological characteristics [34–36]. Our results support the hypothesis advanced by Silva [34] that movements of birds between gallery forests and savannas are the norm within large neotropical savanna regions, and that these movements are adaptive strategies that enable several species to keep viable populations in a heterogeneous and seasonal environment.

Our results reveal that some ecological traits can be used to predict the likelihood of a species to cross boundaries between gallery forests and savannas [7,37]. The most reliable indicator of the likelihood of a species to move across distinctive habitats is its abundance. This result supports the hypothesis that when a species has more individuals in a landscape, the chances of these individuals finding and crossing a boundary between different local ecosystems are higher [33]. Also, species foraging in the upper strata of the vegetation are more likely to cross boundaries than species foraging on the ground, indicating that species that live in the foliage-air interface do not recognize the high contrast that exists between gallery forests and savannas in the same way that species foraging on the ground do. We did not find that body mass was a good predictor of cross-habitat movements, which contrasts with Lees & Peres [37], who found that body mass was the most important predictor for gap-crossing rates among upland forest species.

Moreover, the richness and abundance of spillover species decreased with the distance from the boundary, as well as with the reduction of mean tree height. Our results match the general patterns described by Tubelius et al. [34] for birds in central Brazil, although his work focused solely on forest species moving to savannas, whereas ours includes bidirectional movements. Our results are also consistent with the resource-edge hypothesis [36] that predicts that species richness and abundance peak along the boundaries between ecosystems that have a sharp difference in resource availability, such as gallery forests and savannas. Although forest edges can have a negative effect on species that live in the interior of the forests [38], they are productive spots for spillover bird species because they provide abundant food resources (fruits and insects), nest substrates, and protection against predators and natural fires [39–41]. The direct relationship between mean vegetation height and the amount of species and individuals of spillover species within savannas reinforces the importance of the habitat structure as a key factor in explaining the variation of bird assemblages [42]. Accordingly,, savannas with tall trees are predicted to receive more visits by spillover species than savannas with short trees, and savannas with tall trees near gallery forests are predicted to receive more spillover species than savannas with tall trees distant from gallery forests [40].

We found that there is an intense flow of cross-habitat movements along the boundaries between gallery forests and savannas that extends at least up to 225 m into the savanna. This is an important finding because it provides an estimate of how far spillover species can influence the ecological processes operating at the landscape level. Because they are ecologically versatile, spillover species can play an important role in the exchanges of materials between ecosystems, and thus, influence the dynamics of the location and nature of the ecological boundaries within a landscape [4,6]. The most obvious of these processes is seed dispersal, as seed rains generated by spillover species can facilitate the establishment of forest species in some patches within the savanna matrix and thus, over time, change the landscape configuration. The majority of the spillover species (64.7%) are herbivores or omnivores that can disperse seeds of forest plant species. Some spillover species, such as *Ortalis motmot*, *Pteroglossus aracari*, and *Ramphastos tucanus* have wide bills that allow them to disperse large seeds of forest trees [41–43]. However, most of the spillover species have narrow bills and can only disperse small seeds of pioneer forest plant species deep into the savanna matrix [44]. It is noteworthy that three of the most common spillover species (*Thraupis episcopus*, *Thraupis palmarum*, and *Ramphocelus carbo*) recorded in our study were also the three most important species dispersing seeds from second-growth forests to abandoned pastures in the eastern Amazon, thus influencing plant succession and accelerating forest recovery [4].

We have demonstrated that 88 species of birds crossed the boundaries between gallery forests and savannas in a neotropical savanna landscape, indicating unique and underappreciated biological dynamics that occur along a 225 m wide belt along gallery forests. In order to explain the implications of these findings for conservation planning, the context, limitations of the existing legal framework, and conservation opportunities of this landscape must be considered. The context is that neotropical savannas are under pressure because of the fast expansion of large-scale commercial agriculture everywhere, specifically in South America [45–47]. Although this pressure is more substantial in the Cerrado region, which includes central Brazil, Bolivia, and Paraguay [44], it has also recently reached the Amazonian savannas [48]. The Amapá savannas, the area where we conducted our study, are the most threatened Amazonian savannas because they are located near the coast, and are consequently subject to large infrastructure systems that produce and export agriculture products to the external market [23–25]. Moreover, the major limitation of the existing legal framework is that although several countries have specific laws to protect gallery forests due to their importance for water protection, they do not consider the areas adjacent to them [48]. In the case of Brazil, gallery forests are considered to be Permanent Preservation Areas (Law Nº. 12,651/12), but this law does not protect the entire gallery forest and does not take into account the biological dynamics that exist between forests and savannas. For streams up to 10 m wide (the category in which most of the watercourses in the savannas fit), Brazilian legislation only guarantees the protection of about 30 m on each side. Assuming that the average width of the large forests in our study area (mean = 244 m, SD=97.3 m) well represents the situation of most Amazonian savannas, it becomes clear that most gallery forests and adjacent savannas in these regions are not formally protected.

With respect to conservation opportunities in the landscape, based on the movements of forest birds into savannas, Tubelis et al. [9] suggested that a buffer of 60 m of savannas along the forest boundary is required to maintain the biological dynamics that occur along the gallery forests and savannas. However, our study shows that this buffer should be at least 225 m wide when considering the movements of all spillover species. In the Brazilian context, to add this buffer to gallery forests through legislation change is not feasible from a political viewpoint because recent history shows that achieving consensus among all interest groups on this specific subject is difficult [49]. Hence, new opportunities should be sought. One opportunity within the Brazilian legal framework, that is not available in other countries, is to combine the Permanent Preservation Areas with Legal Reserves, which are defined as portions of rural private property that should be protected or managed sustainably to maintain and restore ecological processes, conserve biodiversity and protect animals and plants [50,51]. According to current legislation, rural properties in savannas within the Amazon should conserve at least 35% of their total area in Legal Reserves, while rural properties in savannas outside the Amazon should protect 20%. However, this system of individually conserving natural ecosystems in rural properties does not necessarily lead to meaningful conservation at the landscape level. In all neotropical savannas, finding a balance between agriculture and conservation demands that land-use planning is carried out at the landscape level by following the principles of sustainable agriculture landscapes [e.g., 52,53] and then implemented at the property level by using existing legal frameworks and other mechanisms, such as payment for ecosystem services [54].

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Supporting Information

S1 Table. Bird species recorded along the forest-savanna boundaries in a tropical savanna landscape in State of Amapá, Brazilian Amazon (see codes)

S2 Table. Average distances (in m) and standard deviation (SD) over which spillover species were observed from the boundary into the savanna in Amapá, Brazil.

S1 Table

Bird species recorded along the forest-savanna boundaries in a tropical savanna landscape in State of Amapá, Brazilian Amazon (see codes)

Family/Species	Habitat Group	Total abundance	Foraging Stratum	Trophic Group	Body Mass (g)
Tinamidae					
Crypturellus erythropus	fo	1	g	her	350
Crypturellus soui	sp	5	g	her	206
Cracidae					
Ortalis motmot	sp	43	ms	her	502
Odontophoridae					
Colinus cristatus	sa	12	g	omn	142.5
Columbidae					
Columbina minuta	sa	9	g	her	33
Columbina passerina	sp	18	g	her	32
Columbina talpacoti	sa	17	g	her	47
Leptotila rufaxilla	sp	12	g	her	153
Leptotila verreauxi	sp	10	g	her	155
Patagioenas cayennensis	sp	92	ms	her	260
Patagioenas speciosa	sp	5	ms	her	261
Zenaida auriculata	sa	44	ms	her	117
Cuculidae					
Coccycua minuta	sp	4	ms	car	30
Coccyzus americanus	sa	2	ms	car	48
Crotophaga ani	sa	8	ms	ins	95
Guira guira	sa	31	ms	omn	140
Piaya cayana	sp	23	ms	ins	118
Trochilidae					
Amazilia fimbriata	sp	15	ms	her	4.3
Amazilia versicolor	sa	1	ms	her	4.3
Anthracothorax nigricollis	sa	2	ms	her	7
Anthracothorax viridigula	sa	1	ms	her	7
Chlorestes notata	sa	5	ms	her	3.8
Chrysolampis mosquitus	sa	14	ms	her	3
Eupetomena macroura	sa	2	ms	her	7.5
Phaethornis ruber	sp	26	ml	her	2.2
Thalurania furcata	sa	2	ms	her	5
Rallidae					
Anurolimnas viridis	sa	2	g	omn	64
Burhinidae					
Burhinus bistriatus	sa	8	g	ins	600
Accipitridae					
Buteogallus meridionalis	sa	8	g	car	960
Buteogallus schistaceus	sa	2	g	car	355

Rupornis magnirostris	sp	13	ms	car	290
Trogonidae					
Trogon violaceus	sa	1	ms	omn	54
Trogon viridis	sp	18	ms	omn	84
Momotidae					
Momotus momota	fo	12	ms	ins	122
Alcedinidae					
Megaceryle torquata	sp	4	g	car	300
Bucconidae					
Bucco tamatia	sp	5	ms	car	36
Chelidoptera tenebrosa	sa	5	ms	ins	35
Notharchus tectus	sa	1	ms	ins	27
Galbulidae					
Galbula galbula	sp	14	ms	ins	29
Ramphastidae					
Pteroglossus aracari	sp	3	ms	omn	280
Ramphastos tucanus	sp	27	ms	omn	600
Picidae					
Campephilus melanoleucos	sp	8	ml	omn	220
Colaptes campestris	sa	11	g	omn	150
Dryobates passerinus	sa	2	ms	ins	30
Dryocopus lineatus	sp	16	ms	ins	200
Picumnus cirratus	sa	1	ms	ins	14
Falconidae					
Caracara cheriway	sa	12	g	car	1310
Falco femoralis	sa	1	ms	car	310
Falco rufigularis	sa	1	ms	car	140
Herpetotheres cachinnans	sp	6	ms	car	505.6
Milvago chimachima	sa	10	ms	car	325
Psittacidae					
Amazona amazonica	sp	41	ms	her	310
Amazona ochrocephala	sp	31	ms	her	530
Ara ararauna	fo	16	ms	her	1125
Ara macao	sp	16	ms	her	1025
Ara severus	sp	27	ms	her	430
Brotogeris versicolurus	sp	28	ms	her	60
Eupsittula aurea	sp	144	ms	her	86.5
Forpus passerinus	sa	31	ms	her	25
Graydidascalus brachyurus	sp	12	ms	her	233
Orthopsittaca manilatus	sp	31	ms	her	370
Psittacara leucophthalmus	sp	58	ms	her	190
Pyrrhura picta	fo	10	ms	her	67
Thamnophilidae					
Cercomacroides tyrannina	sp	21	ms	ins	17
Formicivora grisea	sp	17	ms	ins	11

Formicivora rufa	sa	23	ms	ins	13
Myrmeciza longipes	sp	12	ms	ins	22
Myrmotherula axillaris	fo	7	ms	ins	8
Percnostola rufifrons	sp	6	ms	ins	30
Sclateria naevia	sp	2	ms	ins	22
Taraba major	fo	1	ms	ins	60
Thamnophilus doliatus	sp	12	ms	ins	28
Thamnophilus punctatus	sp	34	ms	ins	20
Furnariidae					
Berlepschia rikeri	fo	3	ms	ins	30
Dendrocincla fuliginosa	fo	7	ms	ins	37
Dendroplex picus	sp	21	ms	ins	40
Glyphorynchus spirurus	sp	6	ms	ins	14
Lepidocolaptes angustirostris	sa	18	ms	ins	1.5
Xiphorhynchus guttatus	sp	21	ms	ins	65
Pipridae					
Chiroxiphia pareola	sp	14	ms	her	19
Manacus manacus	sp	2	ms	omn	12
Pipra aureola	sp	21	ms	omn	15
Tityridae					
Pachyramphus polychopterus	sp	30	ml	ins	20
Tityra cayana	sa	1	ms	omn	69
Tityra semifasciata	fo	4	ms	omn	88
Tyrannidae					
Attila cinnamomeus	sp	8	ms	car	33
Attila spadiceus	sp	3	ms	ins	38
Camptostoma obsoletum	sp	19	ms	omn	9
Elaenia chiriquensis	sa	37	ms	omn	6.3
Elaenia cristata	sa	3	ms	omn	8.3
Elaenia flavogaster	sp	83	ms	omn	1.3
Empidonomus varius	sp	8	ms	ins	25
Legatus leucophaius	sp	7	ms	omn	23
Lophotriccus galeatus	sp	30	ml	ins	10
Megarynchus pitangua	sp	24	ms	omn	62
Myiarchus ferox	sp	15	ms	omn	24
Myiarchus swainsoni	sa	19	ms	omn	3.5
Myiarchus tuberculifer	sa	1	ms	omn	24
Myiarchus tyrannulus	sp	58	ms	omn	9.8
Myiopagis flavivertex	sa	1	ms	ins	11
Myiopagis gaimardii	sp	55	ms	ins	12
Myiozetetes cayanensis	sp	6	ms	ins	29
Phaeomyias murina	sp	16	ms	omn	10
Pitangus sulphuratus	sp	31	ms	omn	63
Rhytipterna simplex	sp	3	ms	ins	32
Sublegatus modestus	sa	18	ms	ins	10.5
Suiriri suiriri	sa	45	ms	omn	16

Todirostrum cinereum	sp	13	ms	ins	7
Todirostrum maculatum	sa	1	ms	ins	7
Todirostrum pictum	sp	3	up	omn	7
Tolmomyias flaviventris	sp	59	ms	omn	14
Tolmomyias poliocephalus	sp	8	ms	omn	11
Tyrannopsis sulphurea	sp	6	ms	omn	40
Tyrannulus elatus	sp	4	up	omn	7
Tyrannus albogularis	sa	3	ms	omn	36.1
Tyrannus melancholicus	sp	70	ms	omn	39
Tyrannus savana	sa	57	ms	omn	42
Xolmis cinereus	sa	1	ms	ins	54
Vireonidae					
Cyclarhis gujanensis	sp	59	ms	ins	28
Hylophilus pectoralis	sp	11	ms	omn	11.5
Vireo chivi	sp	37	ms	omn	15
Polioptilidae					
Polioptila plumbea	sp	74	ms	ins	6.4
Troglodytidae					
Cantorchilus leucotis	sp	27	ms	ins	16
Pheugopedius coraya	fo	1	ms	ins	15
Troglodytes aedon	sp	28	ms	ins	11
Mimidae					
Mimus saturninus	sa	35	g	omn	64.6
Turdidae					
Turdus leucomelas	sp	60	ms	omn	62
Fringillidae					
Euphonia chlorotica	sp	21	ms	her	11
Euphonia violacea	sp	19	ms	omn	14
Passerellidae					
Ammodramus humeralis	sa	104	ms	her	16
Zonotrichia capensis	sa	26	g	omn	20.4
Icteridae					
Cacicus cela	sp	10	ms	her	104
Icterus cayanensis	sp	2	ms	her	42
Leistes militaris	sa	21	ms	her	44
Psarocolius viridis	sp	7	ms	omn	375
Sturnella magna	sa	10	g	omn	97
Cardinalidae					
Piranga flava	sa	31	ms	omn	41.1
Thraupidae					
Coereba flaveola	sp	64	ms	her	9
Conirostrum speciosum	sp	4	ms	ins	9
Cyanerpes cyaneus	fo	3	ms	omn	14
Cypsnagra hirundinacea	sa	27	ms	omn	31.6
Dacnis cayana	sp	17	ms	her	12

Emberizoides herbicola	sa	19	ms	her	24.2
Hemithraupis guira	sa	1	ms	her	10
Nemosia pileata	sp	13	ms	omn	14
Ramphocelus carbo	sp	39	ms	omn	24
Schistochlamys melanopis	sa	4	ms	omn	35
Sporophila angolensis	sp	5	ml	her	13
Sporophila plumbea	sa	14	ms	her	10.3
Stilpnia cayana	sp	99	ms	omn	18.5
Tangara mexicana	sp	20	ms	her	20
Thraupis episcopus	Sp	54	ms	omn	30
Thraupis palmarum	Sp	54	ms	omn	35

Codes: Habitat Group = fo: forest species, sa: savanna species and sp: spillover species; **Foraging Stratum** = g: ground (foraging on the ground), ml: mid-level (foraging levels of the forest understory, edges, at low, medium or high levels in grasses, shrubs or trees by the trunks, branches and bromeliads, but below the canopy), up: upper-level (foraging through the treetops or above the canopy) and ms: multi-strata (foraging in more than one stratum); **Trophic Group** = her: herbivore (diet includes plant materials such as fruit, nectar, plants or seeds), ins: insectivores (arthropods), car: carnivore (includes vertebrates or carrion) and omn: omnivorous (includes on plant and animal source).

S2 Table

Average distance (and standard deviation) that spillover species moved into the savanna matrix in a tropical savanna landscape in State of Amapá, Brazilian Amazon

Family/Species	number observations	mean distance	standard deviation
Tinamidae			
Crypturellus soui	1	25	0
Cracidae			
Ortalis motmot	5	25	0
Columbidae			
Columbina passerina	9	80.6	84.6
Leptotila rufaxilla	3	108.3	144.3
Leptotila verreauxi	4	62.5	75
Patagioenas cayennensis	53	175	138.3
Patagioenas speciosa	2	25	0
Cuculidae			
Coccycua minuta	2	125	141.4
Piaya cayana	12	58.3	49.2
Trochilidae			
Amazilia fimbriata	9	97.2	87
Phaethornis ruber	5	25	0
Accipitridae			
Rupornis magnirostris	10	80	98.5
Trogonidae			
Trogon viridis	6	50	61.2
Alcedinidae			
Megaceryle torquata	2	175	212.1
Bucconidae			
Bucco tamatia	3	25	0
Galbulidae			
Galbula galbula	5	25	0
Ramphastidae			
Pteroglossus aracari	1	25	0
Ramphastos tucanus	11	65.9	91.7
Picidae			
Campephilus melanoleucos	4	62.5	75
Dryocopus lineatus	8	143.8	138.7
Falconidae			
Herpetotheres cachinnans	4	112.5	175
Psittacidae			
Amazona amazonica	4	37.5	25
Amazona ochrocephala	6	166.7	128.1
Ara macao	3	125	173.2

Ara severus	5	95	109.5
Brotogeris versicolurus	3	58.3	57.7
Eupsittula aurea	37	177.7	118.4
Graydidascalus brachyurus	1	75	0
Orthopsittaca manilatus	3	141.7	125.8
Psittacara leucophthalmus	7	189.3	146.4
Thamnophilidae			
Cercomacroides tyrannina	4	25	0
Formicivora grisea	7	60.7	94.5
Myrmeciza longipes	4	25	0
Percnostola rufifrons	1	25	0
Sclateria naevia	1	25	0
Thamnophilus doliatus	5	55	67.1
Thamnophilus punctatus	5	25	0
Furnariidae			
Dendroplex picus	7	89.3	110.7
Glyphorynchus spirurus	2	25	0
Xiphorhynchus guttatus	3	25	0
Pipridae			
Chiroxiphia pareola	5	25	0
Manacus manacus	1	25	0
Pipra aureola	7	25	0
Tityridae			
Pachyramphus polychopterus	13	55.8	85.5
Tyrannidae			
Attila cinnamomeus	1	25	0
Attila spadiceus	2	75	70.7
Camptostoma obsoletum	9	130.6	110.2
Elaenia flavogaster	48	124	107.9
Empidonomus varius	4	50	50
Legatus leucophaius	2	25	0
Lophotriccus galeatus	9	30.6	16.7
Megarynchus pitangua	10	65	69.9
Myiarchus ferox	10	135	110.1
Myiarchus tyrannulus	40	145	118.1
Myiopagis gaimardii	22	54.5	84
Myiozetetes cayanensis	4	50	28.9
Phaeomyias murina	9	69.4	52.7
Pitangus sulphuratus	14	107.1	117
Rhytipterna simplex	2	25	0
Todirostrum cinereum	6	41.7	25.8
Todirostrum pictum	1	25	0
Tolmomyias flaviventris	19	48.7	80.6
Tolmomyias poliocephalus	2	25	0
Tyrannopsis sulphurea	2	25	0

Tyrannulus elatus	1	25	0
Tyrannus melancholicus	40	135	105.1
Vireonidae			
Cyclarhis gujanensis	26	57.7	70.6
Hylophilus pectoralis	7	46.4	39.3
Vireo chivi	11	29.5	15.1
Polioptilidae			
Polioptila plumbea	36	76.4	98.2
Troglodytidae			
Cantorchilus leucotis	10	25	0
Troglodytes aedon	22	145.5	118.2
Turdidae			
Turdus leucomelas	16	65.6	77.9
Fringillidae			
Euphonia chlorotica	9	41.7	35.4
Euphonia violacea	12	87.5	90.8
Icteridae			
Cacicus cela	5	55	44.7
Icterus cayanensis	1	25	0
Psarocolius viridis	1	25	0
Thraupidae			
Coereba flaveola	34	70.6	82.9
Conirostrum speciosum	1	175	0
Dacnis cayana	6	58.3	60.6
Nemosia pileata	4	75	40.8
Ramphocelus carbo	6	58.3	60.6
Sporophila angolensis	2	225	70.7
Stilpnia cayana	52	129.8	108.6
Tangara mexicana	5	65	89.4
Thraupis episcopus	18	86.1	73.9
Thraupis palmarum	18	97.2	91.1

5. CONCLUSÕES

Nosso estudo mostra que há uma dinâmica muito intensa presente nas bordas entre savanas e florestas de galeria em paisagem de savana neotropical. Este fato se deve há uma grande movimentação de aves ocorrendo de forma bidirecional entre estes dois habitats. Além disso, mostramos que o indicador mais confiável da probabilidade de uma espécies mover-se através das bordas é a abundância total, pois quando uma espécie tem mais indivíduos em uma paisagem, maiores são as chances desses indivíduos encontrarem e cruzarem as bordas entre diferentes ecossistemas locais (Wiens 1992a).

O fato de quase 88 espécies registradas em nosso estudo terem conseguido cruzar as bordas entre florestas de galeria e savanas é surpreendente porque as bordas que separam esses dois ecossistemas têm alto contraste. Sendo que da borda da floresta de galeria até os 100 primeiros metros na savana, há uma maior umidade, a riqueza de plantas, tendo uma maior disponibilidade de recursos alimentares como frutos e insetos, e ainda conter abrigos para as aves, local de nidificação, etc, aumentando as chances de permanecerem mais próximas e cruzarem as bordas dos dois habitats.

Além disso, as espécies que forrageam nos estratos superiores da vegetação são mais prováveis de cruzar as bordas do que as espécies de forrageamento no solo, indicando que as espécies que vivem na interface folhagem-ar não reconhecem o alto contraste que existe entre florestas de galeria e savanas na região, da mesma forma que as espécies que procuram alimentos no chão.

Nossos resultados também mostraram que os movimentos de aves entre matas de galeria e savanas são grandes em regiões de savanas amazônicas e que esses movimentos são estratégias adaptativas que permitem que várias espécies mantenham populações viáveis em um ambiente heterogêneo e sazonal (Silva 1995). Além disso, o fluxo intenso de movimentos entre habitats ao longo das fronteiras entre florestas de galeria e savanas se estendem pelo menos até 225 m na savana, sendo que a maioria das espécies de floresta-savana são herbívoros ou onívoros. Essa informação nos revela uma estimativa de até que ponto as espécies de floresta-savana podem influenciar os processos ecológicos no nível da paisagem, pois essas espécies possuem papel fundamental na dispersão de sementes de espécies de plantas florestais em alguns trechos de savanas, prevendo-se com o tempo alterações na paisagem pelos processos de sucessão ecológica.

Por fim, sabendo-se que as savanas neotropicais estão sob pressão por causa da rápida expansão da agricultura comercial em larga escala em todos os lugares da América do Sul, mais recentemente como vem acontecendo nas savanas amazônicas, e a principal limitação da estrutura legal existente, são as leis específicas que protegem as florestas de galeria devido à sua importância para a proteção da água, mas elas não levam em consideram as áreas adjacentes e a dinâmica biológica existente entre florestas e savanas as florestas, e nem a matriz savana que são áreas importantes para a grande diversidade existente. No caso da legislação brasileira, as florestas de galeria são consideradas APP (Lei nº 12.651 / 12), mas vimos essa lei não protege toda a floresta de galeria. Riachos de até 10 m de largura (categoria na qual a maioria dos cursos de água das savanas se encaixa), a legislação brasileira garante apenas a proteção de cerca de 30 m de cada lado, com base em nosso estudo concordamos que a legislação deve ser modificada, e que deveria incluir um buffer com pelo menos 225 m de largura para ser protegido, levando em considerando os movimentos de todas as espécies de transbordamento, que inclui tantos as espécies de aves de floresta que usam as savanas, assim como as espécies de aves da savana que usam as florestas, entre outros grupos faunísticos que se beneficiam de ambos os habitats. Nossa proposta de conservação de áreas mínimas de savana ao longo das florestas de galeria nas savanas neotropicais é importante para que se possam manter biodiversidade e os processos ecológicos nas savanas neotropicais.

6. ANEXO

Comprovante de submissão

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Dr José Maria Cardoso da Silva

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