Universidade de Brasília
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Ecologia

Efeitos da perda de hábitat e fragmentação sobre comunidades de aves e paisagens acústicas do Chaco Paraguaio

Nadia Romina Cardozo Escobar

Brasília, DF - 2022

Universidade de Brasília

Instituto de Ciências Biológicas

Programa de Pós-Graduação em Ecologia

Efeitos da perda de hábitat e fragmentação sobre comunidades de aves e paisagens acústicas do Chaco Paraguaio

Tese apresentada ao Programa de Pós-Graduação em Ecologia
da Universidade de Brasília como requisito necessário
para obtenção do título de Doutora em Ecologia

Orientador: Prof. Dr. Ricardo Bomfim Machado

Brasília, DF - 2022

The individual has always had to struggle to keep from being overwhelmed by the tribe. If you try it, you will be lonely often, and sometimes frightened. But no price is too high to pay for the privilege of owning yourself.

Friedrich Nietzsche

Las aves colorean mi vida con sus cantos. Violeta colorea mi existencia.

Romina

Tese de doutorado

Nadia Romina Cardozo Escobar

Título:

Efeitos da perda de hábitat e fragmentação sobre comunidades de aves e paisagens acústicas do Chaco Paraguaio

Banca examinadora:

Prof. Dr. Ricardo Bomfim Machado
Presidente/Orientador
ZOO/ UnB

Profa. Dra. Mercedes Bustamante
Membro titular
ECL/UnB

Prof. Dr. Gonçalo Ferraz
Membro titular
UFRGS

Dr. Alberto Yanosky
Membro titular
CONACYT

Prof. Dr. Murilo Sversut Dias
Membro Suplente
ECL/UnB

Agradecimentos

Um especial agradecimento aos meus orientadores, que me orientaram durante a execução do projeto, Ricardo Machado que me deu suporte no Brasil, sempre predisposto e paciente. Um especial reconhecimento ao meu co-orientador não oficial, Tobias Kuemmerle que me deu a oportunidade de trabalhar com ele, me recebeu no seu laboratório, me deu suporte em Berlim, obrigada pelos ensinamentos e constante apoio. Foi um prazer trabalhar com vocês.

Aos colegas do Laboratório de Planejamento Sistemático para a Conservação, Lais Brasileiro, Angela Dutra e Edgar Luiz de Lima pela parceria e companhia, assim como aos colegas do Conservation Biogeography Lab da Universidade de Humbold, em especial agradeço a Julieta Decarre, Alfredo Romero-Muñoz e Kathrin Trommler, obrigada pela ajuda durante o processo e pela companhia.

Agradeço muito ao Fernando Andrade e Bárbara Zimbres pelas traduções, orientações e discussões sobre as análises.

Meus caros da equipe de campo Hugo del Castillo, Lucas Cañete que incondicionalmente estiveram comigo todos os dias da coleta. Gostaria de agradecer também à Prof. Mercedes Bustamante que emprestou parte dos equipamentos do seu laboratório para o meu campo, e à Embaixada do Paraguay em Brasília que me ajudou com a burocracia de transporte internacional dos equipamentos de campo.

Agradeço a todos os proprietários que autorizaram a realização do meu trabalho, obrigada pelo interesse e cuidado com nossa equipe durante o trabalho. As pessoas e instituições que apoiaram meu projeto, Green Commodities do Chaco, Cooperativa Neuland, Prof. Andrea Weiler, Fortín Toledo (Proyecto Tagua), Asociación Guyra Paraguay e ao Ministerio del Ambiente y Desarrollo Sostenible de Paraguay.

Agradeço a toda a equipe do Programa de Pós-Graduação em Ecologia, professores e coordenadores, e sou muito grata aos membros da banca examinadora, por terem aceitado o convite e se disponibilizado a contribuir com o trabalho. Enfim, gostaria de agradecer à CAPES pela bolsa de estudos no Brasil, ao DAAD German Academic Exchange Service pela bolsa de estudos na Alemanha e Humboldt-Universität zu Berlin pela acolhida, The Rufford Foundation e o Programa de Pós-graduação em Ecologia (Proex-CAPES) que financiaram meu campo no Paraguay e compra de materiais de campo, e ao Consejo Nacional de Ciencia y Tecnología (CONACYT) do Paraguay a través do Programa Nacional de Incentivo al Investigador, que me deu suporte financeiro na prorrogação do meu doutorado.

Finalmente, e não menos importante, gostaria de agradecer ao meu marido, minha família no Brasil, que me deu suporte e apoio todos estes anos. Um grande agradecimento aos meus pais, que me apoiaram nessa escolha, aos meus irmãos e sobrinhos, aos amigos que fiz durante esses anos e os que permanecem distantes enviando seu apoio.

Sumário

Resumo Geral

A perda de habitat e fragmentação da paisagem permanece como uma das principais ameaças à de perda de biodiversidade, como consequência da expansão da agricultura ao redor do mundo. Entender melhor a importância relativa desses fatores é particularmente urgente para as florestas tropicais e sub tropicais secas do mundo, muitas das quais são pouco estudadas, altamente ameaçadas e estão desaparecendo rapidamente. O Chaco Paraguaio é um *hotspot* global de desmatamento, mas, apesar disso, ainda não está claro como a mudança no uso da terra está impulsionando a mudança de habitat e a perda de biodiversidade nesta região. A conversão do hábitat levou à um aumento do processo de fragmentação e transformação das paisagens, sustentados pelas políticas econômicas e de desenvolvimento. O processo de fragmentação afeta as comunidades de aves e de aves especialistas adaptadas ao ambiente semiárido, uma vez que muda a estrutura da paisagem, reduzindo a superfície de hábitat, a disponibilidade de recursos e alterando o microambiente. Diante disso, a presente Tese discute as respostas das comunidades de aves às mudanças da estrutura da paisagem, assim como às mudanças do microambiente decorrentes da perda de habitat e fragmentação da floresta seca e o uso potencial dos índices acústicos como avaliação rápida das comunidades de aves visando aumentar os estudos em áreas ameaçadas como o Chaco Seco. Esta Tese está dividida em quatro capítulos. O primeiro capítulo corresponde a uma revisão sobre o Chaco Paraguaio, suas ameaças, lacunas do conhecimento e conservação. Os seguintes três capítulos correspondem a estudos empíricos apresentados em forma de manuscritos em inglês. A coleta de campo foi no Chaco Seco Paraguaio durante o final da estação seca em setembro-outubro de 2019, em propriedades privadas dedicadas à pecuária, utilizando gravadores automáticos para identificar as comunidades de aves.

O primeiro capítulo apresenta o Gran Chaco, o Chaco Seco, suas características, ameaças e importância ecológica. Também revisa o contexto ambiental do Chaco Paraguaio, transformação da paisagem, ameaças e estrutura da paisagem. Finalmente, discute as lacunas do conhecimento e as oportunidades de conservação da biodiversidade com ênfases em aves.

O segundo capítulo avaliou os impactos da perda de habitat e fragmentação na diversidade taxonômica, funcional e filogenética das aves. Para isso foram usados modelos lineares generalizados para testar uma série de hipóteses sobre os efeitos da perda de habitat e fragmentação. Foram selecionados 31 pontos de estudo em fragmentos

de florestas e em florestas secas contínuas e foram medidas variáveis estruturais da paisagem a partir de buffers de diferentes escalas. A identificação das aves foi realizada manualmente, escutando as gravações. Nossas análises revelaram que a perda e a fragmentação de habitat afetaram as diferentes facetas da diversidade de aves de forma diferente, com a diversidade funcional e filogenética sendo mais fortemente afetadas pela fragmentação do que a diversidade taxonômica. Também encontramos grandes diferenças na resposta das comunidades de aves à mudança da paisagem ao focar em toda a comunidade de aves versus analisar apenas a comunidade de aves da floresta. Para toda a comunidade de aves, a quantidade e a fragmentação do habitat foram importantes para explicar a variação na diversidade, e a diversidade aumentou com a maior complexidade da paisagem (por exemplo, menor área florestal, maior densidade de borda) nas três facetas da diversidade. Isso foi diferente para as aves florestais, onde a fragmentação florestal foi a variável mais importante explicando a variação na diversidade, e menor cobertura florestal e maior fragmentação florestal foi associada a menor diversidade funcional.

O terceiro capítulo avaliou as respostas das aves ao microambiente medindo a estrutura da vegetação e variáveis ambientais em fragmentos que conectam estruturalmente a paisagem. Foram selecionados 22 corredores florestais distantes, pelo menos, um quilômetro entre si. Em cada um deles, foram medidas variáveis do micro-habitat e do microclima para testar os efeitos do clima e da estrutura da vegetação na composição e na riqueza de aves. Nas análises estatísticas, foram realizadas análises multivariadas e modelos lineares generalizados. A identificação das aves e das comunidades foi realizada manual e automaticamente utilizando índices acústicos. Nossas análises revelaram a importância de corredores florestais, que não apenas conectam a paisagem, mas podem facilitar a movimentação de espécies, possuindo um alto potencial de gerenciamento e planejamento de conectividade. Encontramos diferenças significativas nas comunidades de aves para as mudanças ambientais ao focar em todas as aves ou ao analisar apenas as aves da floresta seca. Para todas as aves, a composição revelou preferências de habitat. Aves de habitats abertos foram positivamente associadas à abertura do dossel, temperatura e umidade relativa do ar, enquanto as aves que evitam ambientes abertos foram positivamente associadas à maior densidade do dossel. As variáveis mais importantes que explicam as variações das aves da floresta seca foram o sub-bosque e a densidade do dossel. A riqueza aumenta com a temperatura para toda a comunidade, mas temperaturas mais altas durante o dia diminuem

a atividade das aves. No geral, mostramos que as diferenças na composição das aves foram associadas a mudanças no dossel, mas a riqueza aumentou com a cobertura do sub-bosque.

O quarto capítulo teve como objetivo principal avaliar o desempenho de índices acústicos na representação da riqueza de aves em florestas continuas e corredores florestais. As comunidades de aves correspondem a duas regiões: 34 pontos de fragmentos e de florestas secas continuas e 22 corredores florestais. Avaliamos o desempenho de dois índices acústicos (índice de diversidade acústica e índice de complexidade acústica). Nossas análises revelaram que os índices acústicos não explicaram a variação geral da riqueza de aves quando incluídos as duas regiões, floresta contínua e corredores florestais. No entanto, ao analisar as comunidades de aves em florestas contínuas e corredores florestais, os índices acústicos refletiram mudanças na riqueza de aves ao longo deste último. Além disso, os índices acústicos capturaram diferenças entre as regiões, com valores pequenos para os corredores florestais e maiores para a floresta contínua. De modo geral, nosso estudo contribui para um campo incipiente sugerindo que os índices acústicos são sensíveis à complexidade da paisagem e, também, a importância em avaliar sua eficácia e as limitações desses índices sob diferentes condições e diferenças ambientais.

Palavras-chaves: Chaco Seco, comunidades de aves, estrutura da paisagem, corredores florestais, microambiente, índices acústicos

General Abstract

Habitat loss and fragmentation due to the expansion of agriculture remains one of the main threats to biodiversity worldwide. Better understanding the relative importance of these factors is particularly urgent for the world’s tropical dry forest, many of which are understudied, highly threatened and rapidly disappearing. The Paraguayan Chaco is a global hotspot of deforestation, but despite this, how changes in land-use drives habitat change and biodiversity loss in this region remains largely unclear. Habitat conversion, supported by economic and developmental policies, has led to an increase in the fragmentation process transforming the landscape. The fragmentation process affects bird communities in general but even more so the communities of specialist birds adapted to the semi-arid environment, changing the landscape structure, reducing the suitable habitat, the availability of resources and altering the microenvironment. In this context, the current work discusses the responses of bird communities to changes in landscape structure, as well as changes in the microenvironment due to habitat loss and fragmentation, and finally evaluates the potential use of acoustic indices as a quick assessment of bird communities, aiming to increase studies in threatened areas such as Chaco Seco. This Thesis is divided into four chapters, the first corresponds to a review of the ecological status of the Paraguayan Chaco, its threats, gaps in knowledge and conservation. The following three chapters correspond to empirical studies presented in manuscripts format. The fieldwork was conducted in private properties dedicated to livestock in the Paraguayan Dry Chaco during the end of the drought season, between September and October 2019, using automatic recorders to identify bird communities.

The first chapter presents the Gran Chaco, the Dry Chaco, its characteristics, threats and ecological importance. It also reviews the environmental context of the Paraguayan Chaco, landscape transformation, threats and landscape structure. Finally, it discusses knowledge gaps and opportunities for biodiversity conservation with an emphasis on birds.

The second chapter evaluates the impacts of habitat loss and fragmentation on the taxonomic, functional and phylogenetic diversity of birds. For this, we used generalized linear models to test a series of hypotheses about the effects of habitat loss and fragmentation on multiple facets of diversity. We selected 31 study points in fragments and continuous dry forests, and structural variables of the landscape were measured from buffers of different scales. Bird identification was performed manually, listening to the

recordings. Our analyzes revealed that habitat loss and fragmentation affected different facets of bird diversity differently, with functional and phylogenetic diversity being more strongly affected by fragmentation than taxonomic diversity. We also found major differences in the response of bird communities to landscape change when focusing on the entire bird community versus focusing on only the forest bird community. For the entire bird community, habitat amount and fragmentation are important in explaining variation in diversity, and diversity generally increases with greater landscape complexity (e.g., less forest area, greater edge density) across all landscapes for all three facets of diversity. This was different for forest birds, where forest fragmentation was the most important variable explaining variation in diversity, and lower forest cover and greater forest fragmentation were associated with lower functional diversity.

The third chapter evaluates the responses of birds to the microenvironment by measuring the vegetation structure and environmental variables in fragments that structurally connect the landscape. We selected 22 forests, in each of which we measured microhabitat and microclimate variables to test the effects of climate and vegetation structure on bird composition and richness using multivariate analysis and generalized linear models. The identification of birds and communities was performed manually and automatically using acoustic indices. Our analyzes revealed the importance of forest corridors, indicating that they not only connect the landscape, but may facilitate the movement of species, having a high potential for connectivity management and landscape planning. We found significant differences in bird communities for environmental changes when focusing on all birds or when looking only at dry forest birds. For all birds, the composition revealed habitat preferences. Birds from open habitats were positively associated with canopy openness, temperature and relative air humidity, while birds that avoid open environments were positively associated with higher canopy density. The most important variables that explain the variations of dry forest birds were understory and canopy density. For the entire community, richness increases with temperature, but higher temperatures during the day decrease bird activity. Overall, we show that differences in bird composition are associated with canopy changes, but richness increased with understory cover.

The fourth chapter aims to evaluate the performance of acoustic indices in the representation of bird richness in continuous forests and forest corridors. The bird communities correspond to two regions, 1) 34 points of fragments and continuous forests and 2) 22 forest corridors. We evaluate the performance of two acoustic indices (acoustic

diversity index and acoustic complexity index). Our analyzes reveal that the acoustic indices do not explain the overall variation in bird richness when including the two regions, continuous forest and forest corridors. However, when analyzing bird communities in continuous forests and forest corridors individually, the acoustic indices reflected changes in bird richness over forest corridors only. In addition, the acoustic indices captured differences between regions, with small values for forest corridors and higher values for continuous forest. Overall, our study contributes to an incipient field suggesting that acoustic indices are sensitive to landscape complexity, yet considering the importance of evaluating their effectiveness and limitations under different conditions and environmental differences.

Keywords: Dry Chaco, bird communities, landscape structure, forest corridors, microenvironment, acoustic indices

Hipóteses

i. A diversidade de aves responde de maneira diferente aos efeitos da perda de hábitat e fragmentação, sendo que toda a comunidade de aves responde positivamente e as aves de floresta respondem negativamente.

   a. *A perda de hábitat e fragmentação levam à heterogeneidade de hábitats incluindo florestas, bordas e áreas abertas que favorecem o estabelecimento de aves generalistas, o que leva a uma maior diversidade taxonómica, funcional e filogenética para toda a comunidade de aves. No entanto, as aves de florestas sendo dependentes da floresta são impactadas negativamente pela perda de hábitat e fragmentação, levando a uma menor diversidade taxonómica, funcional e filogenética.*

ii. As alterações do micro-hábitat e microclima modificam a composição das comunidades de aves em paisagens fragmentadas, principalmente às relacionadas à temperatura, implicando em alterações sobre as atividades das aves.

   a. *A estrutura da vegetação e variáveis ambientais representam um importante fator para a composição e riqueza das comunidades de aves em florestas secas. Mudanças decorrentes de paisagens fragmentadas, dentro de corredores florestais podem promover a alteração da comunidade de aves. Tal efeito será mais evidente com o aumento da temperatura, uma vez que as altas temperaturas reducem as atividades das aves em função de adaptações e restrições fisiológicas relacionadas à floresta seca.*

iii. Os índices acústicos explicam a variação da riqueza de aves em paisagens fragmentadas.

   a. *Os índices acústicos representam uma importante ferramenta para automatização do monitoramento da biodiversidade. Da mesma forma, têm-se mostrado eficazes ao explicar a riqueza de aves em determinados ambientes. Variações da riqueza de aves podem explicar as respostas das aves às mudanças da estrutura da paisagem representada em florestas continuas, fragmentos e corredores florestais. Tal efeito pode ser medido utilizando os índices acústicos que respondem às diferenças entre as regiões.*

Objetivos

Objetivo Geral

Caracterizar os efeitos das mudanças da estrutura da paisagem decorrentes da perda de hábitat e fragmentação na composição e diversidade da comunidade de aves do Chaco Seco Paraguaio, assim como suas potenciais implicações no microambiente e na utilização dos índices acústicos como ferramenta de avaliação rápida.

Objetivos Específicos

i. Descrever os impactos da perda de habitat e fragmentação na diversidade taxonômica, funcional e filogenética das comunidades de aves do Chaco Seco Paraguaio.

ii. Caracterizar as alterações na composição e diversidade (riqueza e abundância) das comunidades de aves ao microambiente representado pela estrutura da vegetação, e caracterizar variáveis ambientais presentes em fragmentos que conectam estruturalmente a paisagem.

iii. Investigar o desempenho de índices acústicos na representação da riqueza de aves em paisagens fragmentadas que incluem florestas continuas, fragmentos e corredores florestais.

Capítulo 1

Conservação das aves em paisagens fragmentadas: uma revisão sobre o processo de perda de habitat e fragmentação do Chaco Paraguaio

Introdução

O Gran Chaco é uma região biogeográfica que forma a Diagonal Seca Sul-Americana (Prado and Gibbs 1993), juntamente com o Cerrado, Caatinga e o Pantanal. O bioma ocupa uma área de 1.066.000 km^2, abrangendo os territórios de quatro países: Argentina (62,19%), Paraguai (25,43%), Bolívia (11,61%) e Brasil (0,77%) (TNC 2005) (Figura 1). A região apresenta uma grande variedade de climas e relevos, que dá origem a uma ampla diversidade de ambientes, pastagens naturais, savanas (secas e inundadas), áreas alagadas, serras e rios, e uma ampla extensão e diversidade de florestas e arbustos (TNC 2005).

A vegetação é determinada, a nível regional, pelas chuvas, existindo duas assembleias principais, estáveis e conspícuas: o Chaco Seco (uma região mais seca na porção nordeste, que possui florestas semidecíduas lenhosas e floresta xerofítica); e o Chaco Úmido (situado na porção sudeste com vegetação pirófita, higrófita e inundáveis) (Navarro et al. 2011).

O Chaco Seco corresponde essencialmente a uma extensão subtropical de uma formação temperada (Navarro et al. 2011). O clima é semiárido, apresentando uma precipitação que varia de 564 a 1103 mm, com um notável gradiente de oeste a leste e de sul a norte (Pennington et al. 2000). A aridez aumenta progressivamente para o oeste, culminando nas áreas mais secas onde o Chaco transita para o sopé dos Andes (Navarro et al. 2011). O bioma pode ser distinguido por sua forte sazonalidade, sendo que a estação chuvosa ocorre de outubro a abril com temperaturas extremamente altas, atingindo até 48,9 °C. Durante o inverno, a vegetação é submetida a baixa umidade do solo, com congelamento por severas geadas (Pennington et al. 2000).

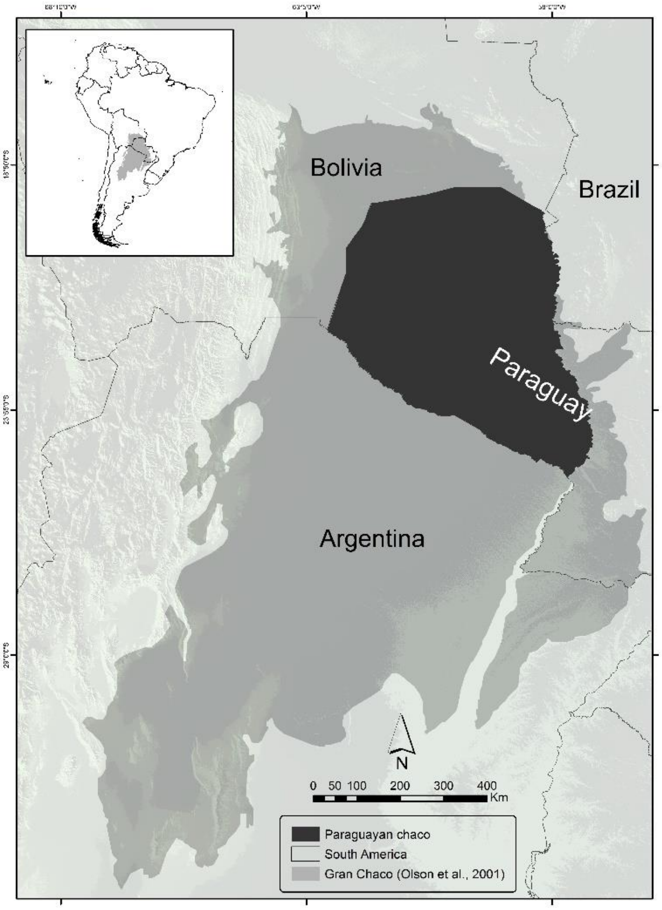


Figura 1. O Gran Chaco é uma região biogeográfica que abrange os territórios de quatro países: Argentina (62,19%), Paraguai (25,43%), Bolívia (11,61%) e Brasil (0,77%) (TNC 2005)

A humanidade modifica o ambiente à medida que a população cresce e as tecnologias de desenvolvimento se expandem; como consequência, os ecossistemas são dominados diretamente pelos humanos. A transformação do solo representa a alteração humana mais substancial do sistema terrestre (Mantyka-Pringle et al. 2015; Tilman et al. 2017). A estreita relação entre fatores bióticos e abióticos sugere que as mudanças climáticas globais e a alteração de hábitat atuarão sinergicamente nas florestas tropicais secas, de modo que, na previsão de impactos futuros sobre a biodiversidade, esses processos devem ser considerados em conjunto (Siyum 2020). O Chaco Seco tem um clima semiárido com um período seco durante os meses frios de inverno. É importante ressaltar que o período seco é caracterizado por uma redução substancial na intensidade e duração dos regimes hidrológicos, traduzindo-se em uma redução da atividade da vegetação (Marchesini et al. 2020). Tais condições restringem as atividades das espécies, reduzem a sobrevivência em altas temperaturas (Woodworth et al. 2018). Além disso, prevê-se que a região experimente mudanças climáticas significativas no futuro (Siyum 2020). As previsões sugerem a ocorrência de eventos secos frequentes e o aumento da temperatura média global, promovendo mudanças ambientais que levam a respostas das espécies em todas as escalas (Walther et al. 2002). Nessas circunstâncias, a cobertura vegetal desempenha um papel fundamental no balanço hídrico durante a estação seca nas regiões semiáridas (Marchesini et al. 2020; Rodriguez et al. 2020). No entanto, a pressão predominante da expansão agrícola continua ameaçando a floresta seca e, portanto, o balanço hídrico regional, incluindo o funcionamento desse ecossistema no longo prazo (Gasparri and Baldi 2013; Rodriguez et al. 2020).

A América Latina e o Caribe têm a maior área de floresta tropical, a maior biodiversidade do mundo, uma grande proporção do estoque global de carbono acima do solo (Laurance et al. 2014; Roque et al. 2018), e áreas protegidas ameaçadas por fatores internos e externos (Lambin and Meyfroidt 2011; Song et al. 2018). A expansão agrícola e as perdas de biodiversidade são mais drásticas nos trópicos, mas há um forte viés de pesquisa predominante para se concentrar nos impactos do uso da terra na biodiversidade em geografias fora dos trópicos (Martin et al. 2012; Trimble and van Aarde 2012). Além disso, a maioria dos estudos dentro dos trópicos se concentrou nas florestas tropicais, enquanto as florestas tropicais secas e savanas permanecem negligenciadas (Portillo-Quintero and Sánchez-Azofeifa 2010; Martin et al. 2012; Pennington et al. 2018; Pendrill et al. 2022). Como resultado, nossa compreensão dos impactos das mudanças no uso da terra agrícola na biodiversidade é parcial para muitas regiões do Neotrópico.

As florestas secas tropicais e subtropicais (florestas secas tropicais ou TDF *tropical dry forest* em inglês) são globalmente difundidas e fornecem importantes serviços ecossistêmicos (Pennington et al. 2018). TDF detêm uma quantidade considerável de carbono e biodiversidade única (Pennington et al. 2018; Siyum 2020). Infelizmente, muitas TDF estão ameaçadas devido à expansão agrícola, bem como à defaunação (Davis et al. 2020; Buchadas et al. 2022). Apesar dessas pressões, a maioria das TDF permanece pouco pesquisadas (Pennington et al. 2018) e pouco protegidas (Pimm et al. 2014), traduzindo-se em barreiras para o planejamento e ação de conservação eficaz (Miles et al. 2006). Este é particularmente o caso da América do Sul, onde menos de 10% das TDF permanece com pouca ou nenhuma presença humana (Portillo-Quintero and Sánchez-Azofeifa 2010; Escribano-Avila et al. 2017; Pennington et al. 2018). Uma das principais ameaças às florestas secas e savanas tropicais é a agricultura, incluindo cultivo e criação de gado, favorecidas pelas condições agroclimáticas nessas regiões. A agricultura tem causado grandes transformações, tanto em períodos históricos quanto em anos mais recentes (Pennington et al. 2018; Buchadas et al. 2022). A mudança no uso da terra é impulsionada por atores orientados para o mercado que expandem a agricultura industrializada para produzir commodities (por exemplo, soja, milho e carne bovina) para os mercados doméstico e internacional (Buchadas et al. 2022). Isso tem causado grande perda da floresta seca e savana tropical e subtropical como o Chaco, Cerrado e Caatinga (Leal et al. 2005; Baldi et al. 2013; Miranda et al. 2019)

O Gran Chaco é a maior região de floresta seca da América do Sul e tem sido particularmente atingido pela expansão agrícola. Estudos constatam que a o aumento da perda de cobertura nativa no Chaco começou no início do ano 2000 (Aide et al. 2013; Vallejos et al. 2015). A expansão generalizada da soja e da pecuária transformou essa região em um *hotspot* global do desmatamento (Hansen et al. 2013; Kuemmerle et al. 2017; Song et al. 2018), porém contém uma biodiversidade ainda pouco estudada. Dentro do Chaco, o desmatamento tem sido mais desenfreado no Paraguai desde 2010 (de la Sancha et al. 2021; Baumann et al. 2022).

Entre os principais fatores que promovem a perda de cobertura nativa no Chaco estão (1) os preços da carne (e.g. preços dos commodities) (Henderson et al. 2021; FAO 2022), (2) as tecnologias (e.g. permite modificar geneticamente a soja para cultivo) (Graesser et al. 2015) e (3) a migração apoiada pela infraestrutura das áreas (e.g. o Chaco Paraguaio recebeu novos imigrantes em busca de oportunidades para aumentar a produção de carne) (Milán and González 2022). Os imigrantes eram basicamente motivados pelas terras baratas, mas com o dinheiro necessário para investir na região considerada hostil pela falta de infraestrutura (Lambin et al. 2001). Este movimento envolve mudanças no desenvolvimento de fronteiras e de políticas por parte dos governos nacionais, que puxam ou empurram os migrantes para áreas pouco ocupadas (Rudel et al. 2009).

Abrangendo uma diversidade de ambientes, de barreiras políticas e geográficas, a perda de cobertura nativa no Chaco acontece de forma diferente em cada país. Embora, desde a década de 1980, o cultivo de soja tenha sido um dos principais fatores de mudança na cobertura da terra no Chaco Argentino, no Chaco Paraguaio o principal fator foi a pecuária (Fehlenberg et al. 2017; Baumann et al. 2022). Entre os fatores limitantes para o cultivo de soja na região, destacam-se o regime de chuvas e a textura do solo (Grau et al. 2005; Gasparri et al. 2015), que exigem mais investimentos para o desenvolvimento dessa prática. No entanto, esse cenário pode mudar no futuro, contribuindo para a expansão da produção de grãos, principalmente apoiado ao padrão de mudanças na precipitação que favorece ao aumento das chuvas, como já observado na Argentina (Zak et al. 2008). Além disso, novas variedades de soja, incluindo cultivares transgênicas resistentes ao glifosato, estão aumentando a produtividade e superando as restrições ambientais, tornando esse empreendimento agrícola muito lucrativo (Grau et al. 2005). Nos últimos anos, no Paraguai, o desmatamento tem sido impulsionado principalmente pela expansão de pastagens plantadas. Na Argentina, os desmatamentos são resultantes da expansão da soja e de pastagens plantadas e na Bolívia pela expansão de pastagens plantadas (Baumann et al. 2022; Pendrill et al. 2022).

Compreender a mudança da biodiversidade como consequência da expansão agrícola não é trivial, porque diferentes aspectos da mudança de hábitat podem impactar a biodiversidade de diferentes maneiras. É importante ressaltar que a expansão agrícola leva tanto à perda de hábitat quanto à fragmentação de hábitat (Fahrig 2003; Foley et al. 2005). A perda de hábitat ameaça espécies conectadas a esse hábitat por meio de declínios populacionais e extinções locais (Haddad et al. 2015; Johnson et al. 2017; Pfeifer et al. 2017). No entanto, à medida que a perda de hábitat ocorre, as paisagens também se tornam mais heterogêneas e fragmentadas, contendo uma maior diversidade de hábitats (Fahrig 2003; Fahrig 2013). Como resultado, espécies que não eram encontradas na paisagem originalmente florestada, podem se estabelecer, o que geraria uma riqueza de espécies estável ou até mesmo crescente (Fahrig et al. 2019). Este aspecto é bastante debatido porque pareceria que pode ser beneficioso, porém espécies dependentes da floresta são as mais prejudicadas do ponto da conservação (Fletcher et al. 2018). Devido a esses efeitos compensatórios no nível da comunidade, separar os efeitos relativos da perda de hábitat *versus* fragmentação tem sido um desafio e o impacto da fragmentação permanece debatido. Vários fatores provavelmente contribuem para um quadro, atualmente, inconclusivo. Primeiro, a fragmentação pode ser espacial e temporalmente dependente, mas isso muitas vezes não é considerado (Haddad et al. 2015; Miller-Rushing et al. 2019). Em segundo lugar, diferentes grupos de espécies, como especialistas *versus* espécies generalistas, podem diferir em suas respostas (Pfeifer et al. 2017; Semper-Pascual et al. 2018), mas muitas vezes não são avaliados separadamente. Terceiro, focar em métricas únicas de fragmentação, como comprimento de borda ou medidas de isolamento, pode não capturar todo o impacto da fragmentação (Pfeifer et al. 2017). Compreender melhor se a fragmentação é importante e se os efeitos da fragmentação são positivos ou negativos são aspectos importantes para a definição de estratégias eficazes de gestão e conservação (Fletcher et al. 2018; Miller-Rushing et al. 2019).

Chaco Paraguaio, oportunidades de conservação

O desmatamento histórico do Chaco Paraguaio começa na região Central, com a chegada e o estabelecimento dos colonos europeus conhecidos como Mennonitas em 1930 (Caldas et al. 2013; Milán and González 2022). O Chaco Central se localiza no centro do Chaco Paraguaio, especificamente no Chaco Seco. A ocupação histórica e o desenvolvimento económico da região se limitaram ao Chaco Central, que representava uma das últimas áreas extensas selvagens intocadas da América Latina, com processos ecossistêmicos intactos no nível da paisagem e mudanças relativamente modestas na cobertura florestal original (Yanosky 2013). A perda de cobertura nativa para a expansão das áreas de cultivo e pecuária se intensificou no início dos anos 2000 (Caldas et al. 2013; Vallejos et al. 2015; Baumann et al. 2022).

O Chaco Paraguaio liderou as taxas de conversão de florestas secas na América do Sul nos últimos anos (Song et al. 2018; Franco-Solís and Montanía 2021), sendo a agricultura extensiva de soja e a pecuária as principais ameaças (Baumann et al. 2022). A mudança no uso da terra (Figura 2) leva à rápida conversão desses ecossistemas para a agricultura por agronegócios nacionais e internacionais, estabelecendo grandes fazendas (Prayogi et al. 2020; Milán and González 2022), principalmente para a produção de carne bovina para mercados internacionais (Baumann et al. 2017; Prayogi et al. 2020; Franco-Solís and Montanía 2021). Entre os principais fatores que promovem a perda de cobertura natural no Chaco Paraguaio estão: preços da terra, regulamentos favoráveis e grandes investimentos em infraestrutura na região (Henderson et al. 2021).

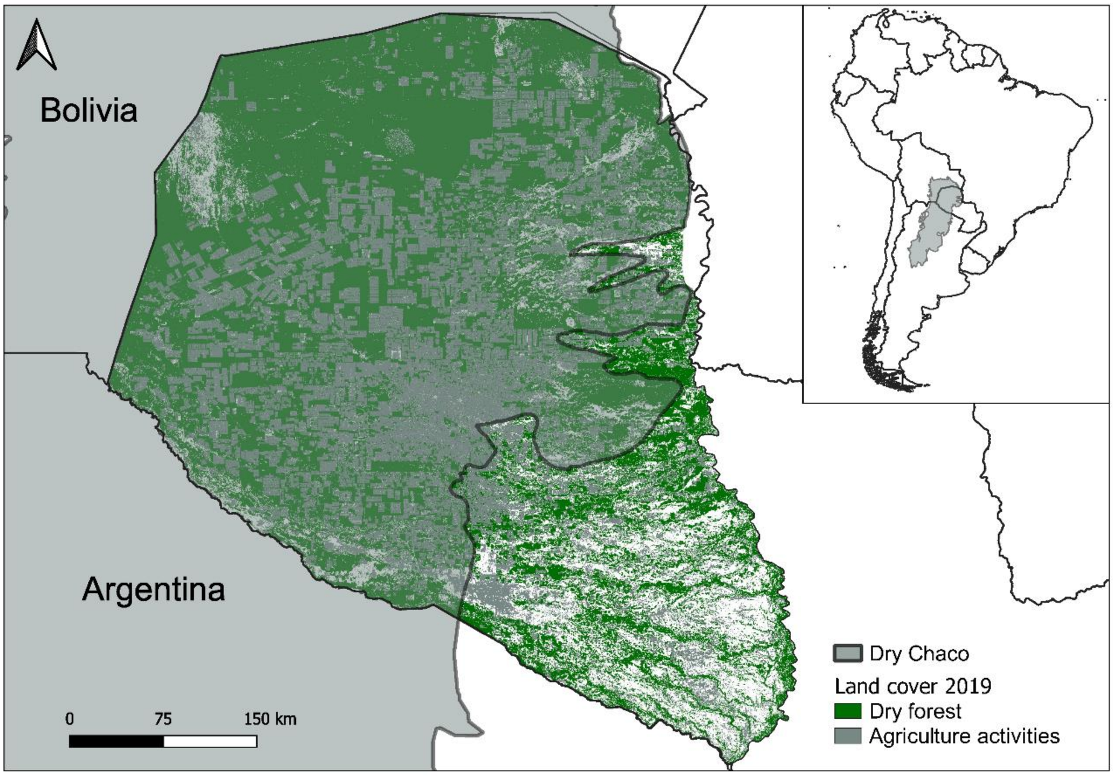


Figura 2. Cobertura da vegetação no Chaco Paraguaio dentro da região Chaco Seco que abrange a Argentina, a Bolívia e o Paraguai. A vegetação representa a floresta seca (verde) e as atividades agrícolas (cinza) desenvolvidas até 2019

A mudança na cobertura da terra no Chaco Paraguaio ocorre devido a várias pressões externas oriundas do agronegócio, como demanda pela produção de grãos e de carne bovina (Pendrill et al. 2022), esta última bastante expressiva em virtude do aumento no preço internacional (Prayogi et al. 2020). Alguns dos impulsionadores mais importantes da transformação da terra são o mercado internacional de alimentos e a política de desenvolvimento no Paraguai (Prayogi et al. 2020; Milán and González 2022), que pretendem promover a expansão da produção pecuária, com o objetivo de duplicar ou triplicar a produção para ajudar a atender à demanda global de carne bovina (Yanosky 2013).

O Chaco Paraguaio contém diversas dinâmicas de desmatamento. O desmatamento no Chaco Central leva a fragmentos pequenos e isolados de florestas remanescentes (Mereles and Rodas 2014). Em contraste, blocos maiores de vegetação natural permanecem na paisagem no norte do Chaco paraguaio, onde a fronteira agrícola atualmente se expande (Vallejos et al. 2015). Atualmente, está vigente a Resolução N 303/04, que define como áreas agrícolas ou fazendas de gado deveriam ser organizadas na paisagem. Antes dessa legislação ser implantada, que se refere ao desenvolvimento histórico do Chaco Central, os proprietários de terras não tinham a obrigação de apresentar às autoridades locais um plano de ocupação para suas propriedades rurais. Por essa razão, é bastante comum observar grandes blocos de terra dominados por atividades agrícolas na região. Esta legislação específica contribuiu expressivamente para ter uma paisagem agrícola mais homogênea, como discutido em Baumann et al. (2022).

A configuração da paisagem é em parte determinada por leis estabelecidas pelo Governo do Paraguai, sendo várias leis elaboradas para proteger a vegetação natural e os recursos florestais. A Lei 542/95 estabelece 25% de superfície de proteção por lei para as propriedades privadas. O Decreto 18.831/86 (Milán and González 2022) exige aos proprietários privados, com mais de 100 ha, a manutenção de uma estreita faixa de floresta entre as parcelas agrícolas, devendo medir pelo menos 100 m de largura. Tais faixas são localmente denominadas de “quebra-ventos”, que têm como objetivo principal conter a pressão do vento e evitar erosões. Este aspecto confere a singularidade à paisagem do Chaco Paraguaio. Embora não haja evidências até o momento de que essas faixas contribuam para proteger a biodiversidade, não pode ser descartado sua importância como elementos florestais que conectam estruturalmente a paisagem.

Os quebra-ventos estão localizados ao longo de caminhos, estradas e bordas de uma propriedade. Eles podem contribuir potencialmente para a dispersão e movimentação de pequenos organismos, armazenamento de carbono e manutenção do microclima (Wang et al. 2001). Hoje em dia, no entanto, a rápida expansão da agricultura e pecuária levou a uma perda massiva da vegetação natural e o cumprimento da legislação está sendo negligenciado. O desmatamento histórico do Chaco Seco, especificamente no Chaco Central (Mereles and Rodas 2014), promoveu uma disposição desordenada dos quebra-ventos legalmente exigidos, sendo que em muitas partes da paisagem há uma inobservância clara da lei ou falta de vegetação natural entre parcelas onde há um uso consolidado da terra (Kriese et al. 2022; Milán and González 2022). No entanto, essas faixas devem fornecer uma oportunidade para manter a conectividade funcional da paisagem por meio de corredores.

A maior parte da vegetação natural do Chaco Paraguaio está desprotegida, pois as áreas protegidas correspondem a apenas 16,2% da região (Nori et al. 2016). A maior pressão de mudança da cobertura vegetal incide sobre as áreas mais importantes para os vertebrados endêmicos no Gran Chaco, os que permanecem fora das áreas protegidas (Nori et al. 2016). Entre os vertebrados mais ameaçados do Chaco estão os mamíferos que sofrem pela perda de hábitat (Romero-Muñoz et al. 2019; Semper-Pascual et al. 2020; Semper-Pascual et al. 2021) e práticas de caça (Saldivar-Bellassai et al. 2021), como a onça pintada (*Panthera onca*), tamanduá-bandeira (*Myrmecophaga tridactyla*) e taguá (*Catagonus wagneri*). Suas populações estão concentradas nas grandes áreas naturais, a maioria delas áreas protegidas que estão ficando isoladas, em meio a fragmentos que estão perdendo conectividade (de la Sancha et al. 2021; Thompson et al. 2022). Diante da preocupação sobre a conectividade estrutural da paisagem e visando conectar as áreas protegidas do Chaco Paraguaio, a criação de corredores naturais baseado em áreas de importância para as espécies tem sido uma das estratégias de conservação mais sugeridas (Mereles et al. 2019).

As aves tropicais são um grupo de foco interessante para entender os efeitos da mudança de hábitat na biodiversidade. As aves são relativamente fáceis de monitorar e sua taxonomia, filogenia, características e atributos funcionais estão bem documentadas (Sekercioglu 2006; Jetz et al. 2012). Da mesma forma, as aves são bons indicadores de mudança da paisagem, pois muitas delas têm associações claras com hábitats específicos e respondem rapidamente às mudanças no ambiente (Gregory et al. 2005; Vandewalle et al. 2010). A perda de hábitat, como em todas as espécies, afeta as populações menores de aves, às vezes colocando as populações em uma trajetória de extinção local (Hanski 1998; Wiens 1999). A fragmentação do hábitat exacerba esta tendência com o isolamento de subpopulações, bem como através de efeitos de borda, como aumento da predação de ninhos, menor sucesso reprodutivo devido a distúrbios humanos ou parasitismo (Bierregaard, et al. 1992; Wiens 1999; Sodhi and Smith 2007). Finalmente, as aves são um grupo taxonômico, funcional e filogenético diverso e, portanto, um grupo de foco interessante para análises em nível de comunidade (Tobias et al. 2022). No entanto, como essas facetas da diversidade são impactadas pela mudança no uso da terra ainda é pouco compreendida em muitas regiões do mundo (Sekercioglu 2012; Haddad et al. 2015; Li et al. 2020).

A alta diversidade de espécies de aves e suas adaptações, histórias de vida e mobilidade permitem às aves regularem uma diversidade de processos ecossistêmicos, mas também que respondam rapidamente às mudanças nos recursos (Gregory et al. 2005; Vandewalle et al. 2010). As preferencias e requerimentos do hábitat levam a diferenciar as aves como especialistas e generalistas. As aves generalistas podem estar em todos os tipos de ambientes, sem restrições, incluindo florestas fechadas, bordas de florestas e áreas abertas. Já as especialistas de floresta dependem da floresta e não são encontradas em outros ambientes, o que leva essas últimas a serem mais susceptíveis às mudanças na cobertura da vegetação. As aves fornecem uma ampla gama de serviços ecossistêmicos, exibindo a mais variada gama de funções ecológicas entre os vertebrados (Sekercioglu 2006). Os serviços ecossistêmicos, incluem serviços culturais, de regulação (dispersão de sementes, polinização, controle de pragas, eliminação de carcaças e de resíduos) e serviços de apoio (deposição de nutrientes, engenharia de ecossistemas) (Sekercioglu et al. 2004; Sekercioglu 2006; Whelan et al. 2008).

Existem aproximadamente 500 espécies de aves no Gran Chaco (TNC 2005) e 18 delas são reconhecidas como endêmicas da região (Short 1975). Alguns estudos avaliaram como a expansão agrícola impactou a biodiversidade de aves no Chaco Argentino, descobrindo que tanto a perda de hábitat quanto a fragmentação afetam as comunidades de aves (Dardanelli et al. 2006). Além disso, a conversão para agricultura intensificada resulta, particularmente, no declínio da riqueza de aves (Mastrangelo and Gavin 2014; Macchi et al. 2020). No entanto, diferenças importantes foram encontradas para paisagens onde as terras agrícolas se expandem *versus* paisagens onde a pecuária se expande (Torres et al. 2014; Macchi et al. 2015; Macchi et al. 2020), e as respostas no nível da comunidade variaram acentuadamente com a escala espacial das avaliações (Semper-Pascual et al. 2021).

Apesar dos estudos citados, os efeitos relativos da perda de hábitat versus fragmentação de hábitat nas comunidades de aves do Chaco permanecem incertos, e outras facetas de diversidade além da riqueza taxonômica (ou seja, diversidade funcional e filogenética) permanecem em grande parte não estudadas. Além disso, não há estudos sobre o Chaco Paraguaio, que sofreu a perda florestal mais drástica recentemente. O Chaco Paraguaio difere do Chaco Argentino de maneiras importantes, inclusive no tamanho e distribuição espacial dos campos, o principal fator imediato do desmatamento (ou seja, pecuária, não soja) e no planejamento do uso da terra e políticas de conservação (Vallejos et al. 2015). A extrapolação de outros contextos socioecológicos para o Chaco Paraguaio é, portanto, provavelmente, injustificada, de forma que estudos que abordem essa lacuna de conhecimento regional são necessários.

Referências

Aide TM, Clark ML, Grau HR, López-Carr D, Levy M a., Redo D, Bonilla-Moheno M, Riner G, Andrade-Núñez MJ, Muñiz M. 2013. Deforestation and Reforestation of Latin America and the Caribbean (2001-2010). Biotropica [Internet].

45(2):262–271. https://doi.org/10.1111/j.1744-7429.2012.00908.x

Baldi G, Verón SR, Jobbágy EG. 2013. The imprint of humans on landscape patterns and vegetation functioning in the dry subtropics. Glob Chang Biol. 19(2):441–458. https://doi.org/10.1111/gcb.12060

Baumann M, Gasparri NI, Buchadas A, Oeser J, Meyfroidt P, Levers C, Romero-Muñoz A, le Polain de Waroux Y, Müller D, Kuemmerle T. 2022. Frontier metrics for a process-based understanding of deforestation dynamics. Environ Res Lett. https://doi.org/10.1088/1748-9326/ac8b9a

Baumann M, Israel C, Piquer-Rodríguez M, Gavier-Pizarro G, Volante JN, Kuemmerle T. 2017. Deforestation and cattle expansion in the Paraguayan Chaco 1987–2012. Reg Environ Chang. 17(4):1179–1191. https://doi.org/10.1007/s10113-017-1109-5

Bierregaard, RO, Lovejoy TE, Kapos V, Hutchings RW. 1992. The Biological Dynamics of Tropical Rainforest Fragments. Bioscience. 42(11):859–866. https://doi.org/10.2307/1312085

Buchadas A, Baumann M, Meyfroidt P, Kuemmerle T. 2022. Uncovering major types of deforestation frontiers across the world’s tropical dry woodlands. Nat Sustain. https://doi.org/10.1038/s41893-022-00886-9

Caldas M, Goodin D, Sherwood S, Campos Krauer JM, Wisely SM. 2013. Land-cover change in the Paraguayan Chaco: 2000–2011. J Land Use Sci [Internet].(April):1–18. https://doi.org/10.1080/1747423X.2013.807314

Dardanelli S, Nores ML, Nores M. 2006. Minimum area requirements of breeding birds in fragmented woodland of Central Argentina. Divers Distrib. 12(6):687–693. https://doi.org/10.1111/j.1472-4642.2006.00266.x

Davis KF, Koo HI, Dell’Angelo J, D’Odorico P, Estes L, Kehoe LJ, Kharratzadeh M, Kuemmerle T, Machava D, Pais A de JR, et al. 2020. Tropical forest loss enhanced by large-scale land acquisitions. Nat Geosci [Internet]. 13(7):482–488. https://doi.org/10.1038/s41561-020-0592-3

Escribano-Avila G, Cervera L, Ordóñez-Delgado L, Jara-Guerrero A, Amador L, Paladines B, Briceño J, Parés-Jiménez V, Lizcano DJ, Duncan DH, Iván Espinosa C. 2017. Biodiversity patterns and ecological processes in Neotropical dry forest: the need to connect research and management for long-term conservation. Neotrop Biodivers [Internet]. 3(1):107–116. https://doi.org/10.1080/23766808.2017.1298495

Fahrig L. 2003. Effects of Habitat Fragmentation on Biodiversity. Annu Rev Ecol Evol Syst. 34:487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fahrig L. 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. J Biogeogr. 40(9):1649–1663. https://doi.org/10.1111/jbi.12130

Fahrig L, Arroyo-Rodríguez V, Bennett JR, Boucher-Lalonde V, Cazetta E, Currie DJ, Eigenbrod F, Ford AT, Harrison SP, Jaeger JAG, et al. 2019. Is habitat fragmentation bad for biodiversity? Biol Conserv [Internet]. 230(October 2018):179–186. https://doi.org/10.1016/j.biocon.2018.12.026

FAO. 2022. Statistic Division production of livestock and crops. Food Agric Organ United Nations.:https://www.fao.org/faostat/en/#data/PP/visualize.

Fehlenberg V, Baumann M, Gasparri NI, Piquer-Rodriguez M, Gavier-Pizarro G, Kuemmerle T. 2017. The role of soybean production as an underlying driver of deforestation in the South American Chaco. Glob Environ Chang [Internet]. 45(April):24–34. https://doi.org/10.1016/j.gloenvcha.2017.05.001

Fletcher RJ, Didham RK, Banks-Leite C, Barlow J, Ewers RM, Rosindell J, Holt RD, Gonzalez A, Pardini R, Damschen EI, et al. 2018. Is habitat fragmentation good for biodiversity? Biol Conserv [Internet]. 226(April):9–15. https://doi.org/10.1016/j.biocon.2018.07.022

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, et al. 2005. Global consequences of land use. Science (80-) [Internet]. 309(5734):570–574. https://doi.org/10.1126/science.1111772

Franco-Solís A, Montanía C V. 2021. Dynamics of deforestation worldwide: A structural decomposition analysis of agricultural land use in South America. Land use policy [Internet]. 109:105619. https://doi.org/10.1016/j.landusepol.2021.105619

Gasparri NI, Baldi G. 2013. Regional patterns and controls of biomass in semiarid woodlands: Lessons from the Northern Argentina Dry Chaco. Reg Environ Chang. 13(6):1131–1144. https://doi.org/10.1007/s10113-013-0422-x

Gasparri NI, Grau HR, Sacchi LV. 2015. Determinants of the spatial distribution of cultivated land in the North Argentine Dry Chaco in a multi-decadal study. J Arid Environ [Internet].:1–9. https://doi.org/10.1016/j.jaridenv.2015.05.005

Graesser J, Aide TM, Grau HR, Ramankutty N. 2015. Cropland/pastureland dynamics and the slowdown of deforestation in Latin America. Environ Res Lett

[Internet]. 10(3):034017. https://doi.org/10.1088/1748-9326/10/3/034017

Grau HR, Gasparri NI, Aide TM. 2005. Agriculture expansion and deforestation in seasonally dry forests of north-west Argentina. Environ Conserv. 32(2):140–148. https://doi.org/10.1017/S0376892905002092

Gregory RD, Van Strien A, Vorisek P, Meyling AWG, Noble DG, Foppen RPB, Gibbons DW. 2005. Developing indicators for European birds. Philos Trans R Soc B Biol Sci. 360(1454):269–288. https://doi.org/10.1098/rstb.2004.1602

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, et al. 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. Sci Adv [Internet]. [accessed 2017 May 3] 1(2):1–9. https://doi.org/10.1126/sciadv.1500052

Hansen MC, Potapov P V, Moore R, Hancher M, Turubanova S a, Tyukavina a, Thau D, Stehman S V, Goetz SJ, Loveland TR, et al. 2013. High-resolution global maps of 21st-century forest cover change. Science [Internet]. 342(2013):850–3. https://doi.org/10.1126/science.1244693

Hanski I. 1998. Metapopulation dynamics. Nature. 396(6706):41–49. https://doi.org/10.1038/23876

Henderson J, Godar J, Frey GP, Börner J, Gardner T. 2021. The Paraguayan Chaco at a crossroads: drivers of an emerging soybean frontier. Reg Environ Chang. 21(3). https://doi.org/10.1007/s10113-021-01804-z

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and time. Nature. 491(7424):444–448. https://doi.org/10.1038/nature11631

Johnson CN, Balmford A, Brook BW, Buettel JC, Galetti M, Guangchun L, Wilmshurst JM. 2017. Biodiversity losses and conservation responses in the Anthropocene. Science (80-). 356(6335):270–275. https://doi.org/10.1126/science.aam9317

Kriese J, Hoeser T, Asam S, Kacic P, Da Ponte E, Gessner U. 2022. Deep Learning on Synthetic Data Enables the Automatic Identification of Deficient Forested Windbreaks in the Paraguayan Chaco. Remote Sens. 14(17). https://doi.org/10.3390/rs14174327

Kuemmerle T, Baldi G, Camino M, Cuellar E, Cuellar RL, Decarre J, Díaz S, Gasparri I, Giordano AJ, Leynaud G, et al. 2017. Forest conservation : Remember Gran Chaco Forest conservation : Humans ’ handprints. Science (80-). 355(6324):465–467.

de la Sancha NU, Boyle SA, McIntyre NE, Brooks DM, Yanosky A, Cuellar Soto E, Mereles F, Camino M, Stevens RD. 2021. The disappearing Dry Chaco, one of the last dry forest systems on earth. Landsc Ecol. 36(10):2997–3012. https://doi.org/10.1007/s10980-021-01291-x

Lambin EF, Meyfroidt P. 2011. Global land use change, economic globalization, and the looming land scarcity. Proc Natl Acad Sci U S A. 108(9):3465–3472. https://doi.org/10.1073/pnas.1100480108

Lambin EF, Turner BL, Geist HJ, Agbola SB, Angelsen A, Folke C, Bruce JW, Coomes OT, Dirzo R, George PS, et al. 2001. The causes of land-use and land-cover change : moving beyond the myths. Glob Environ Chang. 11:261–269. https://doi.org/0959-3780/01/$

Laurance WF, Sayer J, Cassman KG. 2014. Agricultural expansion and its impacts on tropical nature. Trends Ecol Evol [Internet]. 29(2):107–116. https://doi.org/10.1016/j.tree.2013.12.001

Leal IR, Da Silva JMC, Tabarelli M, Lacher TE. 2005. Changing the course of biodiversity conservation in the caatinga of northeastern Brazil. Conserv Biol. 19(3):701–706. https://doi.org/10.1111/j.1523-1739.2005.00703.x

Li D, Olden JD, Lockwood JL, Record S, McKinney ML, Baiser B. 2020. Changes in taxonomic and phylogenetic diversity in the Anthropocene: Changes in biodiversity. Proc R Soc B Biol Sci. 287(1929). https://doi.org/10.1098/rspb.2020.0777rspb20200777

Macchi L, Decarre J, Goijman AP, Mastrangelo M, Blendinger PG, Gavier-Pizarro GI, Murray F, Piquer-Rodriguez M, Semper-Pascual A, Kuemmerle T. 2020. Trade-offs between biodiversity and agriculture are moving targets in dynamic landscapes. J Appl Ecol.(May):1–10. https://doi.org/10.1111/1365-2664.13699

Macchi L, Grau HR, Phalan B. 2015. Agricultural production and bird conservation in complex landscapes of the dry Chaco. J Land Use Sci. 11(2):188–202. https://doi.org/10.1080/1747423X.2015.1057244

Mantyka-Pringle CS, Visconti P, Di Marco M, Martin TG, Rondinini C, Rhodes JR. 2015. Climate change modifies risk of global biodiversity loss due to land-cover change. Biol Conserv [Internet]. 187:103–111. https://doi.org/10.1016/j.biocon.2015.04.016

Marchesini VA, Nosetto MD, Houspanossian J, Jobbágy EG. 2020. Contrasting hydrological seasonality with latitude in the South American Chaco: The roles of climate and vegetation activity. J Hydrol [Internet]. 587(November 2019):124933. https://doi.org/10.1016/j.jhydrol.2020.124933

Martin LJ, Blossey B, Ellis E. 2012. Mapping where ecologists work: Biases in the global distribution of terrestrial ecological observations. Front Ecol Environ. 10(4):195–201. https://doi.org/10.1890/110154

Mastrangelo ME, Gavin MC. 2014. Impacts of agricultural intensification on avian richness at multiple scales in Dry Chaco forests. Biol Conserv [Internet]. 179:63–71. https://doi.org/10.1016/j.biocon.2014.08.020

Mereles MF, Céspedes G, Cartes JL, Goerzen R, Egea-Elsam J De, Rodríguez L, Yanosky A, Villalba L, Weiler A, Cacciali P. 2019. Biological Corridors as a Connectivity Tool in the Region of the Great American Chaco: Identification of Biodiversity Hotspots in the Ecoregions of the Paraguayan Chaco. Res Ecol [Internet]. 2(1):27–36. https://doi.org/10.30564/re.v2i1.1324

Mereles MF, Rodas O. 2014. Assessment of rates of deforestation classes in the Paraguayan Chaco (Great South American Chaco) with comments on the vulnerability of forests fragments to climate change. Clim Change [Internet]. [accessed 2014 Nov 20] 127(1):55–71. https://doi.org/10.1007/s10584-014-1256-3

Milán MJ, González E. 2022. Beef–cattle ranching in the Paraguayan Chaco: typological approach to a livestock frontier. Environ Dev Sustain [Internet].(0123456789). https://doi.org/10.1007/s10668-022-02261-2

Miles L, Newton AC, DeFries RS, Ravilious C, May I, Blyth S, Kapos V, Gordon JE. 2006. A global overview of the conservation status of tropical dry forests. J Biogeogr. 33(3):491–505. https://doi.org/10.1111/j.1365-2699.2005.01424.x

Miller-Rushing AJ, Primack RB, Devictor V, Corlett RT, Cumming GS, Loyola R, Maas B, Pejchar L. 2019. How does habitat fragmentation affect biodiversity? A controversial question at the core of conservation biology. Biol Conserv. 232:271–273. https://doi.org/10.1016/j.biocon.2018.12.029

Miranda J, Börner J, Kalkuhl M, Soares-Filho B. 2019. Land speculation and conservation policy leakage in Brazil. Environ Res Lett. 14(4). https://doi.org/10.1088/1748-9326/ab003a

Navarro G, Molina JA, Vega S. 2011. Soil factors determining the change in forests between dry and wet Chacos. Flora Morphol Distrib Funct Ecol Plants [Internet]. 206(2):136–143. https://doi.org/10.1016/j.flora.2010.09.002

Nori J, Torres R, Lescano JN, Cordier JM, Periago ME, Baldo D. 2016. Protected areas and spatial conservation priorities for endemic vertebrates of the Gran Chaco, one of the most threatened ecoregions of the world. Divers Distrib. 22(12):1212–1219. https://doi.org/10.1111/ddi.12497

Pendrill F, Gardner TA, Meyfroidt P, Persson UM, Adams J, Azevedo T, Lima MGB, Baumann M, Curtis PG, De Sy V, et al. 2022. Disentangling the numbers behind agriculture-driven tropical deforestation. Science (80-). 377(6611). https://doi.org/10.1126/science.abm9267

Pennington RT, Lehmann CER, Rowland LM. 2018. Tropical savannas and dry forests. Curr Biol [Internet]. 28(9):R541–R545. https://doi.org/10.1016/j.cub.2018.03.014

Pennington TR, Prado DE, Pendry CA. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. J Biogeogr [Internet]. 27(2):261–273. https://doi.org/10.1046/j.1365-2699.2000.00397.x

Pfeifer M, Lefebvre V, Peres CA, Banks-Leite C, Wearn OR, Marsh CJ, Butchart SHM, Arroyo-Rodríguez V, Barlow J, Cerezo A, et al. 2017. Creation of forest edges has a global impact on forest vertebrates. Nature [Internet]. 551(7679):187–191. https://doi.org/10.1038/nature24457

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science (80-). 344(6187). https://doi.org/10.1126/science.1246752

Portillo-Quintero CA, Sánchez-Azofeifa GA. 2010. Extent and conservation of tropical dry forests in the Americas. Biol Conserv [Internet]. 143(1):144–155. https://doi.org/10.1016/j.biocon.2009.09.020

Prado DE, Gibbs PE. 1993. Patterns of species distributions in the Dry Seasonal Forests of South America. Missouri Bot Gard Press. 80(4):902–927.

Prayogi AW, Cangara AR, Badu MN, Baharuddin A, Marifat IDN. 2020. The impacts of Paraguayan charcoal export to European markets upon deforestation of Paraguay’s Chaco forest. IOP Conf Ser Earth Environ Sci. 575(1). https://doi.org/10.1088/1755-1315/575/1/012243

Rodriguez P, Giménez R, Nosetto MD, Jobbágy EG, Magliano PN. 2020. Changes in water fluxes partition related to the replacement of native dry forests by crops in the Dry Chaco. J Arid Environ. 183(June).

https://doi.org/10.1016/j.jaridenv.2020.104281

Romero-Muñoz A, Torres R, Noss AJ, Giordano AJ, Quiroga V, Thompson JJ, Baumann M, Altrichter M, McBride R, Velilla M, et al. 2019. Habitat loss and overhunting synergistically drive the extirpation of jaguars from the Gran Chaco. Divers Distrib [Internet]. 25(2):176–190. https://doi.org/10.1111/ddi.12843

Roque FDO, Menezes JFS, Northfield T, Ochoa-Quintero JM, Campbell MJ, Laurance WF. 2018. Warning signals of biodiversity collapse across gradients of tropical forest loss. Sci Rep [Internet]. 8(1):1–7. https://doi.org/10.1038/s41598-018-19985-9

Rudel TK, Schneider L, Uriarte M, Ii BLT, Defries R, Lawrence D, Geoghegan J, Hecht S, Ickowitz A, Lambin EF, et al. 2009. Agricultural intensification and changes in cultivated areas , 1970 – 2005. 106(49):20675–20680.

Saldivar-Bellassai S, Feldpausch-Parker A, Giordano AJ, Frair J. 2021. Hunting practices and harvest of peccaries in the northern Paraguayan Dry Chaco. Biol Conserv [Internet]. 256(June 2020):109059. https://doi.org/10.1016/j.biocon.2021.109059

Sekercioglu CH. 2006. Increasing awareness of avian ecological function. Trends Ecol Evol. 21(8):464–471. https://doi.org/10.1016/j.tree.2006.05.007

Sekercioglu CH. 2012. Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. J Ornithol. 153(SUPPL. 1):153–161. https://doi.org/10.1007/s10336-012-0869-4

Sekercioglu CH, Daily GC, Ehrlich PR. 2004. Ecosystem consequences of bird declines. 101(52). https://doi.org/10.1073/pnas.0408049101

Semper-Pascual A, Burton C, Baumann M, Decarre J, Gavier-Pizarro G, Gómez-Valencia B, Macchi L, Mastrangelo ME, Pötzschner F, Zelaya P V., Kuemmerle T. 2021. How do habitat amount and habitat fragmentation drive time-delayed responses of biodiversity to land-use change? Proc R Soc B Biol Sci. 288(1942). https://doi.org/10.1098/rspb.2020.2466

Semper-Pascual A, Decarre J, Baumann M, Camino M, Di Blanco Y, Gómez-Valencia B, Kuemmerle T. 2020. Using occupancy models to assess the direct and indirect impacts of agricultural expansion on species' populations. Biodivers Conserv. 29(13):3669–3688. https://doi.org/10.1007/s10531-020-02042-1

Semper-Pascual A, Macchi L, Sabatini FM, Decarre J, Baumann M, Blendinger PG, Gómez-Valencia B, Mastrangelo ME, Kuemmerle T. 2018. Mapping extinction debt highlights conservation opportunities for birds and mammals in the South American Chaco. J Appl Ecol. 55(3):1218–1229. https://doi.org/10.1111/1365-2664.13074

Short L. 1975. Zoogeographic Analysis of the South American Chaco Avifauna. Bull Am Museum Nat Hist. 154:163–352.

Siyum ZG. 2020. Tropical dry forest dynamics in the context of climate change: syntheses of drivers, gaps, and management perspectives. Ecol Process. 9(1). https://doi.org/10.1186/s13717-020-00229-6

Sodhi NS, Smith KG. 2007. Conservation of tropical birds: Mission possible? J Ornithol. 148(SUPLL. 2):305–309. https://doi.org/10.1007/s10336-007-0180-y

Song X-P, Hansen MC, Stehman S V., Potapov P V., Tyukavina A, Vermote EF, Townshend JR. 2018. Global land change from 1982 to 2016. Nature [Internet]. https://doi.org/10.1038/s41586-018-0411-9

Thompson JJ, Velilla M, Cabral H, Cantero N, Bonzi VR, Britez E, Campos Krauer JM, McBride RT, Ayala R, Cartes JL. 2022. Jaguar (Panthera onca) population density and landscape connectivity in a deforestation hotspot: The Paraguayan Dry Chaco as a case study. Perspect Ecol Conserv.(xxxx). https://doi.org/10.1016/j.pecon.2022.09.001

Tilman D, Clark M, Williams DR, Kimmel K, Polasky S, Packer C. 2017. Future threats to biodiversity and pathways to their prevention. Nature. 546(7656):73–81. https://doi.org/10.1038/nature22900

TNC. 2005. Evaluacion ecorregional del Gran Chaco Americano. Fundación. Buenos Aires.

Tobias JA, Sheard C, Pigot AL, Devenish AJM, Yang J, Sayol F, Neate-Clegg MHC, Alioravainen N, Weeks TL, Barber RA, et al. 2022. AVONET: morphological, ecological and geographical data for all birds. Ecol Lett. 25(3):581–597. https://doi.org/10.1111/ele.13898

Torres R, Gasparri NI, Blendinger PG, Grau HR. 2014. Land-use and land-cover effects on regional biodiversity distribution in a subtropical dry forest: A hierarchical integrative multi-taxa study. Reg Environ Chang [Internet]. 14(4):1549–1561. https://doi.org/10.1007/s10113-014-0604-1

Trimble MJ, van Aarde RJ. 2012. Geographical and taxonomic biases in research on biodiversity in human-modified landscapes. Ecosphere. 3(12):art119.

https://doi.org/10.1890/es12-00299.1

Vallejos M, Volante JN, Mosciaro MJ, Vale LM, Bustamante ML, Paruelo JM. 2015. Transformation dynamics of the natural cover in the Dry Chaco ecoregion: A plot level geo-database from 1976 to 2012. J Arid Environ [Internet]. 123(1700):3–11. https://doi.org/10.1016/j.jaridenv.2014.11.009

Vandewalle M, de Bello F, Berg MP, Bolger T, Dolédec S, Dubs F, Feld CK, Harrington R, Harrison PA, Lavorel S, et al. 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. Biodivers Conserv. 19(10):2921–2947. https://doi.org/10.1007/s10531-010-9798-9

Walther G, Post E, Convey P, Menzel A, Parmesank C, Beebee TJC, Fromentin J, I OH, Bairlein F. 2002. Ecological response to recent climate cnahge. Nature. 416:389–395.

Wang H, Takle ES, Shen J. 2001. Mathematical Modeling and Computer Simulations of Turbulent Flows. Annu Rev Fluid Mech [Internet]. 33(1):549–586. http://www.annualreviews.org/doi/10.1146/annurev.fluid.33.1.549

Whelan CJ, Wenny DG, Marquis RJ. 2008. Ecosystem Services Provided by Birds. Ann N Y Acad Sci [Internet]. 1134(1):25–60. https://doi.org/10.1196/annals.1439.003

Wiens JA. 1999. Habitat fragmentation: island v landscape perspectives on bird conservation. [place unknown].

Woodworth BK, Norris DR, Graham BA, Kahn ZA, Mennill DJ. 2018. Hot temperatures during the dry season reduce survival of a resident tropical bird. Proc R Soc B Biol Sci. 285(1878). https://doi.org/10.1098/rspb.2018.0176

Yanosky A. 2013. Paraguay’s Challenge of Conserving Natural Habitats and Biodiversity with Global Markets Demanding for Products. Conserv Biol Voices from Trop.:113–119. https://doi.org/10.1002/9781118679838.ch14

Zak MR, Cabido M, Cáceres D, Díaz S. 2008. What Drives Accelerated Land Cover Change in Central Argentina? Synergistic Consequences of Climatic, Socioeconomic, and Technological Factors. Environ Manage [Internet]. 42(2):181–189. https://doi.org/10.1007/s00267-008-9101-y

Capítulo 2

Impacts of habitat loss and habitat fragmentation on multiple facets of avian diversity in a global deforestation hotspot

Abstract

Tropical deforestation is a main driver of biodiversity loss, but the relative importance of habitat loss versus habitat fragmentation remains debated. Better understanding the relative importance of these factors is particularly urgent for the world's tropical dry forest, many of which are understudied, highly threatened and rapidly disappearing. The Paraguayan Chaco is a global hotspot of deforestation, but despite this, how land-use change is driving habitat change and biodiversity loss in this region remains largely unclear. Building on a unique, field-based bird community dataset, we used generalized linear models to test a series of hypotheses on the effects of habitat loss and habitat fragmentation on taxonomic, functional and phylogenetic diversity. Our analyses revealed that habitat loss and fragmentation affected the different facets of avian diversity differently, with functional and phylogenetic diversity being more strongly affected by fragmentation than taxonomic diversity. We also found major differences in the response of bird communities to landscape change when focusing on the entire bird community vs. analyzing the community of forest birds only. For the entire bird community, habitat amount and fragmentation where both important for explaining variation in diversity, and diversity generally increased with higher landscape complexity (e.g., lower forest area, higher edge density) across all three facets of diversity. This was different for forest birds, where forest fragmentation was the most important variable explaining variation in diversity, and less forest cover and higher forest fragmentation was associated with lower functional diversity. Overall, our study adds to a growing body of evidence suggesting that landscape change does not necessarily lead to overall diversity loss, but rather triggers turnover in community composition. We highlight that this includes a substantial loss of forest birds, many of which are of conservation concern in this deforestation hotspot. Likewise, our study highlights the need for and benefit of analyzing multiple facets of biodiversity, particularly functional diversity, to understand how deforestation impacts on biodiversity – in the Chaco and other understudied tropical dry forests.

Keywords: taxonomic diversity, functional diversity, phylogenetic diversity, dry forest, forest birds

Introduction

Biodiversity is degraded in many parts of the world and a key driver of this trend is habitat destruction due to agricultural expansion and intensification (Tilman et al. 2017). This is particularly so in the tropics and subtropics, where agriculture continues to expand into remaining natural areas (Lambin and Meyfroidt 2011; Song et al. 2018), which harbor high and unique biodiversity (Laurance et al. 2014; Roque et al. 2018). Agricultural expansion and biodiversity losses are most drastic in the tropics, yet there is a strong prevailing research bias to focus on land-use impacts on biodiversity in geographies *outside* the tropics (Martin et al. 2012; Trimble and van Aarde 2012). Moreover, within the tropics, most studies focused on rainforests, whereas tropical dry forests and savannas remain heavily neglected (Portillo-Quintero and Sánchez-Azofeifa 2010; Martin et al. 2012; Pennington et al. 2018; Pendrill et al. 2022). As a result, our understanding of the impacts of agricultural land-use change on biodiversity is partial for many regions.

Understanding biodiversity change in the face of agricultural expansion is not trivial, because different aspects of habitat change might impact biodiversity in different ways. Importantly, agricultural expansion leads to both, habitat loss and habitat fragmentation (Fahrig 2003; Foley et al. 2005). Regarding habitat loss, there is now considerable empirical evidence, as well as theoretical underpinnings, suggesting that habitat destruction threaten species connected to this habitat through population declines and local extinctions (Haddad et al. 2015; Johnson et al. 2017; Pfeifer et al. 2017). However, as habitat loss ensues, landscapes also become more heterogeneous and fragmented, containing a higher diversity of habitats (Fahrig 2003, 2013). As a result, species that were not found in this landscape when it was entirely forested may be able to establish themselves, potentially leading to a stable or even increasing diversity (Fahrig et al. 2019). Due to such compensatory effects at the community level, disentangling the relative effects of habitat loss vs. fragmentation has been challenging and the impact of fragmentation *per se* remains debated. Several factors likely contribute to the currently inconclusive picture. First, fragmentation may be spatially and temporally dependent, yet this is often not considered (Haddad et al. 2015; Miller-Rushing et al. 2019). Second, different species groups, such as specialist vs. generalist species might differ in their responses (Pfeifer et al. 2017; Semper-Pascual et al. 2018), but are often not assessed separately. Third, focusing on single measures of fragmentation, such as edge length or isolation measures, may not capture the full impact of fragmentation (Pfeifer et al. 2017).

Better understanding whether fragmentation matters and whether the effects of fragmentation are positive or negative is important to identify effective management and conservation strategies (Fletcher et al. 2018; Miller-Rushing et al. 2019).

A further complication for unravelling the effect of habitat loss and fragmentation is that they might impact different facets of biodiversity differently (Cernansky 2017; Pollock et al. 2020; Semper-Pascual et al. 2021), yet most studies have explored the relative effects of habitat loss vs. habitat fragmentation focusing on taxonomic richness only. Importantly, facets other than taxonomic diversity could be more directly related to environmental changes, and thus more useful to understand the relative impacts of habitat loss and habitat fragmentation. Functional diversity, which measures the diversity of traits is an indicator of ecosystem health and resilience, could be particularly promising (Flynn et al. 2011), as land-use change has been shown to reduce functional diversity (Laliberté et al. 2010) but it would depends of the traits used (Flynn et al. 2009). Similarly, phylogenetic diversity, which reflects the diversity of evolutionary heritage (Flynn et al. 2011) has been suggested to better capture the impacts of land-use change on biodiversity (Haddad et al. 2015; Li et al. 2020). However, studies systematically exploring how landscape transformation impacts on biodiversity across all facets of diversity are rare, particularly in the tropics and from places where landscape transformation occurs rapidly. Yet it is exactly for these places where empirical studies are most urgently needed.

Tropical birds are an interesting focus group for understanding the effects of habitat change on biodiversity. Birds are relatively easy to monitor and their taxonomy, phylogeny, traits and functional roles are well documented (Sekercioglu 2006; Jetz et al. 2012). Likewise, birds are good indicators of landscape change, as many of them have clear habitat associations and they respond quickly to changes in the environment (Gregory et al. 2005; Vandewalle et al. 2010). Habitat loss, like in all species, leads to smaller populations of birds, sometimes putting populations on a trajectory towards local extinction (Hanski 1998; Wiens 1999). Habitat fragmentation exacerbates this trend through the isolation of sub-populations, as well as via edge effects, such as increased nest predation, lower breeding success due to human disturbance, or parasitism (Bierregaard, et al. 1992; Wiens 1999; Sodhi and Smith 2007). Finally, birds are a taxonomically, functionally and phylogenetically diverse taxon, and thus an interesting focus group for community-level analyses (Tobias et al. 2022). Yet how these facets of diversity are impacted by land-use change remains poorly understood for many regions of the world (Sekercioglu 2012; Haddad et al. 2015; Li et al. 2020).

Tropical and sub-tropical dry forest (hereafter: tropical dry forests or TDF) are globally widespread and provide key ecosystem services (Pennington et al. 2018). TDF hold a considerable amount of carbon and unique biodiversity (Pennington et al. 2018; Siyum 2020). Unfortunately, many TDF are threatened due to agricultural expansion (Davis et al. 2020; Buchadas et al. 2022), as well as defaunation (Dirzo et al. 2014; Pennington et al. 2018). Despite these pressures, most TDF remain under-researched (Pennington et al. 2018) and weakly protected (Pimm et al. 2014), translating into barriers for effective conservation planning and action (Miles et al. 2006). This is particularly the case for South America, where less than 10% of TDF remain with little or no human pressure (Portillo-Quintero and Sánchez-Azofeifa 2010; Escribano-Avila et al. 2017; Pennington et al. 2018). The Gran Chaco is the largest dry forest ecoregion in South America, and has been particularly hard-hit by agricultural expansion recently. Widespread soybean and cattle ranching expansion have turned this region a global deforestation (Hansen et al. 2013; Song et al. 2018; Kuemmerle et al. 2017). Within the Chaco, deforestation has been most rampant in Paraguay since 2010 (de la Sancha et al. 2021; Baumann et al. 2022).

A few studies have assessed how agricultural expansion has impacted on avian biodiversity in the Argentinian Chaco, finding that both habitat loss and fragmentation reshape bird communities (Dardanelli et al. 2006) and that particularly the conversion to intensified agriculture results in declining avian richness (Mastrangelo and Gavin 2014; Macchi et al. 2020). However, important differences were found for landscapes where croplands expand vs. landscapes where ranching expands (Torres et al. 2014; Macchi et al. 2015, 2020), and community-level responses varied markedly with the spatial scale of assessments (Semper-Pascual et al. 2021). Despite these studies, the relative effects of habitat loss vs. habitat fragmentation on the Chaco's bird communities remains unclear, and diversity facets other than taxonomic richness (i.e., functional and phylogenetic diversity) remain largely unstudied. In addition, there are no studies at all so far from the Paraguayan Chaco, which has undergone the most drastic forest loss recently. The Paraguayan Chaco differs from the Argentinean Chaco in major ways, including in the size and spatial distribution of fields, the main proximate driver of deforestation (i.e. cattle ranching, not soybean) and in land-use planning and conservation policies (Vallejos et al. 2015). Extrapolating from other social-ecological contexts to the Paraguayan Chaco is therefore likely unjustified, and studies addressing this regional knowledge gap are needed.

Our main goal was to assess the relative effects of habitat loss and habitat fragmentation on different facets of avian diversity in the Paraguayan Chaco – one of the world's hottest deforestation hotspots (Song et al. 2018; Franco-Solís and Montanía 2021). Specifically, we asked the following research questions:

1. How do habitat amount and fragmentation affect avian richness in the Paraguayan Chaco?
2. Do these effects differ when comparing the entire bird community vs. the community of forest specialist birds only?
3. Are there differences between taxonomic diversity, functional diversity and phylogenetic diversity in their relationship with habitat amount and fragmentation?

Materials and methods

Study area

The Gran Chaco is a biogeographic region comprising the Wet Chaco and the Dry Chaco ecoregions. The Dry Chaco, one of the largest tropical dry forests in South America, extends over mostly flat terrain across an area of 840,000 km² in Argentina, Paraguay and Bolivia. The Dry Chaco contains a mosaic of xerophytic vegetation formations, including dry forests, scrublands and savannas (Pennington et al. 2000; Werneck 2011). The soils in the Chaco are generally suitable for agriculture, and mainly derive from fluvial pedogenesis in the north and from eolic sediments and loess in the south (Navarro et al. 2011). The climate is semiarid with summer maxima of up to 49 °C. There is a strong east-west rainfall gradient (450–700 mm), as well as marked seasonality, with a dry season in the winter/spring and a rainy season in the summer/autumn. Vegetation can be subject to low soil moisture and freezing temperatures during the dry season and waterlogging and extremely high temperatures during the rainy season (Pennington et al. 2000).

Our study area was located in the heart of the Paraguayan Dry Chaco (Fig. 1), a region where natural vegetation is dominated by xeromorphic forest and scrubland (Mereles and Rodas 2014). Most of the natural vegetation in the Paraguayan Chaco is unprotected (16.2% of protected areas; Nori et al. 2016). Land-use change leads to the rapid conversion of these ecosystems to agriculture by domestic and international agribusinesses, establishing large farms (Milán and González 2022), mainly for producing beef for international markets (Baumann et al. 2017; Franco-Solís and Montanía 2021). Despite this general land-use trend, the outcomes for landscape configuration in the Paraguayan Chaco are diverse. For instance, in the central Paraguayan Chaco, deforestation leads to small and isolated fragments of remaining forests (Mereles and Rodas 2014), whereas in the northern Paraguayan Chaco, larger blocks of natural vegetation remain in the landscape (Vallejos et al. 2015).

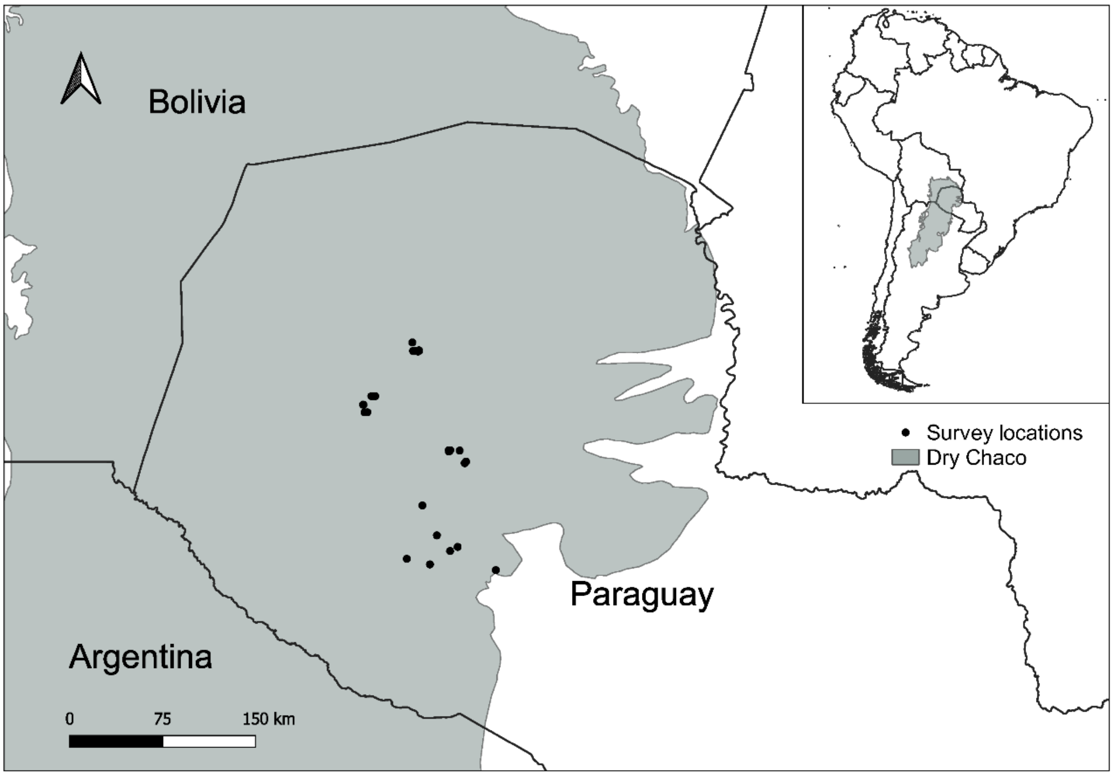


Fig. 1 Study area in the Paraguayan Dry Chaco with the 31 survey locations, with a gray line is the Dry Chaco of South America.

Bird surveys

To sample bird communities in the Paraguayan Chaco, we used sound recorders. This non-invasive method is useful for estimating biodiversity abundance and occurrence (Hill et al. 2018), minimizes human disturbance and interferences, and allows for longer term monitoring of a wide range of vocal species, such as birds (Sugai et al. 2019; Pérez-Granados and Traba 2021). Birds were surveyed at n=31 sites in continuous forest patches as well as smaller forest fragments inside larger cattle ranches. Sites were selected based on landscape characteristics to include diverse landscape configurations, both in the central and northern Paraguayan Chaco (Fig. 1). We recorded bird calls during September and October of 2019 during two days at each site, coinciding with the end of the dry season, a time period when most birds in this region initiate breeding. Each recording consisted of 10-minute samples (wave format 48 MHz and 16 bits) during the peak of avian vocal activity (i.e., 05:00 to 08:30 in the morning and 16:00 to 19:00 in the evening) to detect both diurnal and nocturnal birds. Bird species were identified by the same observer (the lead author), listening to the recordings (1360 independent recordings, 20 recordings per day) assisted by the stereo spectrogram program Raven Pro 1.6 (Center for Conservation Bioacoustics 2019). We only registered persistent singing and excluded songs of birds flying through (e.g., flying parrots) and used bird song repositories for species identification (i.e., Xeno-Canto, www.xeno-canto.org; Macaulay Library, www.macaulaylibrary.org), as well as consulted with experts on bird songs from the region.

Calculation of facets of bird diversity

We constructed two sets of response variables for our analyses. The first consisted of all birds (hereafter: all birds), including both forest specialist and generalist species that use a variety of habitats including closed forest, forest edges and open areas. The second set was based only on forest specialist birds (hereafter: forest birds) that prefer closed forests and are rarely found in other habitat types. We classified forest birds based on published habitat associations (Parker III et al. 1996; Dardanelli et al. 2006; Semper-Pascual et al. 2018) (Table A1 Supplementary material).

For each bird community set (all bird and forest birds only), we calculated taxonomic diversity, functional diversity and phylogenetic diversity. Taxonomic diversity was derived as the local richness (i.e., alpha diversity per site). For functional diversity, we first constructed a table summarizing functional characteristics for each species, included 1) diet, 2) foraging stratum, 3) body mass and 4) habitat preferences (see Table S1 in the Supplementary Material). We then calculated a dissimilarity matrix using Gower’s measure of distance (Pavoine et al. 2009). As our measure of functional diversity, we calculated the functional dispersion index (Laliberte and Legendre 2010). This index measures the mean distance in the multidimensional trait space of individual species to the centroid of all species, where the multidimensional functional space is obtained through a principal coordinate analysis based on the Gower dissimilarity matrix (R package “FD”, Laliberte and Legendre 2010). Finally, to calculate phylogenetic diversity, we followed Faith’s approach, which represents the minimum total length of the phylogenetic tree's branches of the species within each community (Faith 1992). We extracted a set of 1,000 avian phylogenies from http://birdtree.org based on the Ericson backbone (Jetz et al., 2012; Ericson et al. 2006 downloaded on 12/11/2021 for all birds and 16/02/2022 for forest birds). We then built a phylogenetic consensus tree for the species in our community using the function averageTree in the R package “phytools” (Revell 2012). From this phylogenetic tree, we calculated phylogenetic diversity using the R package “picante” (Kembel et al. 2010).

Landscape-scale predictor variables

To evaluate the influence of habitat amount and habitat fragmentation on bird diversity, we calculated predictor variables representing both aspects of landscape change. We adopted an approach where we captured diverse landscape in terms of their structure at one point in time (as the bird sampling cannot be carried out retrospectively). As these landscapes represent different stages of deforestation, assessing the responses of bird community to diversity in landscape configuration allows to estimate the effects of land-use change on birds, analogue to a space for time approach. We calculated predictors for differently sized buffers (0.5 km, 1 km and 3 km) around our 31 sample sites, with the position of the sound recorder at the center of the buffer ring. We selected 0.5 km as the minimum buffer, because this area represent the sensitivity of the sound recorder to detect birds, as well as 1-km and 3-km buffers as the areas around the plot in which birds move and forage, depending on home range size (Semper-Pascual et al. 2021).

To capture habitat amount, we calculated forest area (i.e., as a proxy for the extent of natural habitat), based on land-cover/use maps generated from Landsat TM and ETM+ image composites at 30-m resolution (Baumann et al. 2022). We used the map for the year matching our bird surveys. This map is a highly accurate representation of forest cover, with a user’s and producer’s accuracy of 92% and 93%, respectively (Baumann et al. 2022). To capture habitat fragmentation, we selected two complementary landscape metrics: patch density and edge density (Table 1). Patch density measures the number of patches in the landscape (i.e., our circular buffer around a sampling site) and edge density measures the proportion of edge forest as a share of the total landscape area (McGarigal 2014). For the latter, we used an edge width of 30m (1 pixel) in line with similar work in the Argentinean Chaco (Semper-Pascual et al. 2021). We checked all predictor variables for collinearity using Pearson’s correlation coefficient and all variable pairs were $r< |0.7|$ (Fig. A1).

Table 1. Predictor variables used to measure habitat amount and habitat fragmentation as well as a-priori hypothesis related to these variables.

	Description	*Value*	*Hypotheses*
Habitat amount			
Forest area	Amount of forest in the landscape (i.e., buffer area)	Hectares (ha)	H1: Diversity of all birds is negatively related to forest area for all facets. H2: Diversity of forest birds is positively related to forest area across facets.
Habitat fragmentation			
Edge density	Edge length as a share of total landscape area	Meters per hectare (m/ha)	H3: Fragmentation is positively related to the diversity of all birds. H4: The diversity of forest birds decreases with increasing edge density for all facets.
Patch density	Number of patches in 100 hectares	Number per 100 hectares (n/100ha)	H5: The diversity of all birds increases with a patchier landscape across facets H6: The diversity of forest birds decreases with higher patch density.

Statistical models

All analyses were performed in the R statistical software (R Core Team 2021). The first step in our analyses was to explore bivariate relationships between response and predictor variables using scatterplots (Fig. A2, A3, A4). Second, we assessed the correlation between our three predictors variables, measured at three scales, and our three response variables (i.e., biodiversity facets) using univariate GLMs (i.e., a total of 3 x 3 x 3 =27 models) (Table S2). To compare among these models, we calculated Akaike’s Information Criterion corrected for small samples (AICc).

Next, we performed a model selection to test all combination of best-performing predictor variables for each facet of avian diversity using the R package “glmulti” (Calcagno and de Mazancourt 2010). We selected the best-performing model based on the AICc, considering models with ΔAICc <2 as having equally strong empirical support and plausibility (Burnham and Anderson, 2002; Burnham et al. 2011). We averaged these best-performing models using the R package “MuMIn” (Barton 2022) in order to derive conditional average coefficients. To evaluate the importance of each predictor in these averaged models, we used the sum of Akaike weights (w_i) of each candidate model in which the predictor appeared (Burnham and Anderson, 2002). We also derived graphical relationships between predictors and responses for all significant predictors for the best-performing models (Mayorga et al. 2020).

Results

Taxonomic diversity across all our 31 sites was 99 bird species for the entire avian community. Most of the bird species surveyed were resident species, with the exception of one migratory species (i.e., *Tyrannus melancholicus*). In total, we identified 63 forest bird species (i.e., 64% of all species recorded) and 36 species were generalist birds. Eight species (8%) were ubiquitous, occurring in all sites we surveyed, of which six were forest birds (i.e., *Lepidocolaptes angustirostris, Hemitriccus margaritaceiventer, Chunga burmeisteri, Cyclarhis gujanensis, Furnarius cristatus, Myiarchus tyrannulus*) and two were generalist bird species (i.e., *Patagioaenas picazuro* and *Paroaria coronata*). Phylogenetic diversity for all birds was higher than for the community of forest birds. This was different for functional diversity, where the community of forest birds had a higher diversity than the community of all birds (Fig. 2).

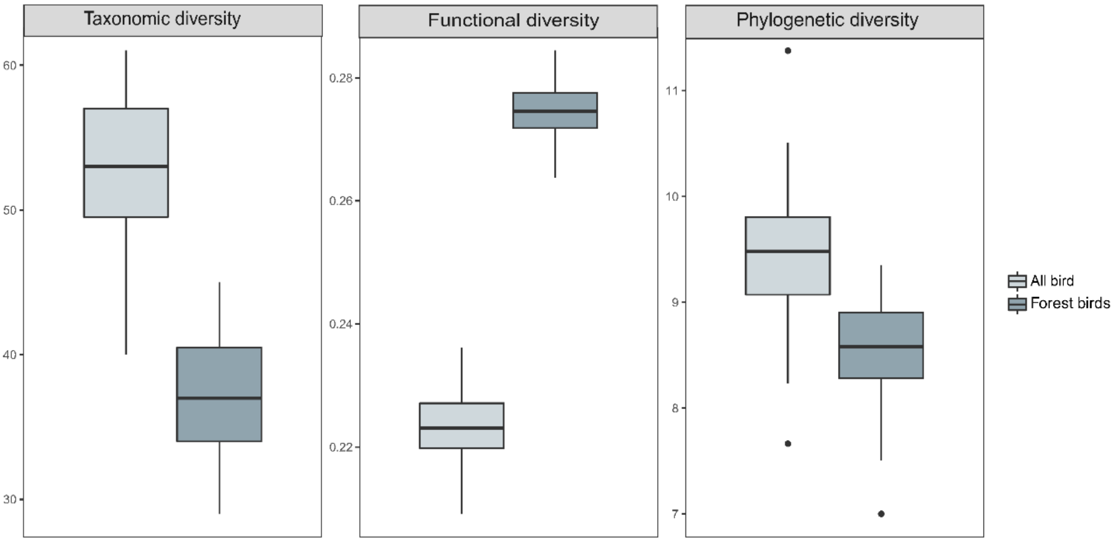


Fig. 2. Distribution of the three facets of avian diversity across 31 sampling sites in the tropical dry forest of the Paraguayan Chaco. Facets were calculated for the community of all birds that were recorded and for forest specialist birds only. Taxonomic diversity refers to richness, functional diversity refers to diversity of avian traits, and

phylogenetic diversity refers to diversity of avian evolutionary heritage (see Methods). Box plots show median, quartiles, as well as maximum and minimum values.

Correlating our response variables with our predictor variables in bivariate models showed diverse responses (Fig. A2 - A4). For the community of all birds, forest area did not correlate appreciably with taxonomic diversity, whereas we found a weak positive relation for functional diversity at some scales (r<0.30 at 3-km scale) and a negative relation for phylogenetic diversity (Fig. A2). Regarding our fragmentation metrics, patch density had a weak positive correlation with taxonomic diversity (r<0.30 at 3-km scale) and with our measure of phylogenetic diversity (r<0.30; Fig. A3). Edge density had a weak positive correlation with functional diversity (r<0.30) and a scale-dependent correlation with taxonomic and phylogenetic diversity (i.e., negative 0.5-km and 1-km scales and positive at the 3-km scale; Fig. A4). For the community of forest birds, results differed from the patterns found for the community of all birds. Forest area was generally not highly correlated with our diversity facets (Fig. A2). Patch density was weakly correlated with taxonomic diversity, had a negative correlation with functional diversity (i.e., 1-km and 3-km scales), and a positive correlation with phylogenetic diversity (Fig. A3). Finally, edge density was positively correlated with taxonomic diversity and phylogenetic diversity, particularly at broader scales (i.e., 3-km; Fig. A4).

Comparing relationships across the spatial scales used to summarize predictor variables around our sampling plots showed marked differences among scales. Generally, relationships between our predictor variables and diversity in all facets for both communities (i.e., all birds and forest birds) were scale-dependent and best-explained when predictors were summarized at a broader scale (i.e., 3-km; Table 2, Table S2). However, no scale was clearly superior across all facets and predictor variables in our univariate models. We therefore decided to allow for the inclusion of variables summarized at different scales in our models, using a model selection routine. This allowed to select the best-performing combination of predictor variables for each facet of avian diversity, for both communities, while accounting for the multi-scalar nature of the impacts of habitat change on bird diversity (Table 2).

This multi-variate and multi-scalar GLMs generally explained bird diversity across our study sites well, with the best model receiving high support (i.e., high Akaike weights) for most diversity facets (Table 2). When explaining diversity facets for the community of all birds, our best-performing model explained taxonomic diversity well based on fragmentation metrics along (i.e., edge density, Fig. 3A). Our best models explaining functional and phylogenetic diversity, however, included the forest area and edge density predictors. Generally, for all birds, diversity increased with increasing landscape complexity (e.g., lower forest area, higher edge density) across facets of diversity (Table 2, Table 3).

For the community of forest birds, our final GLMs also explained general diversity patterns well, with fragmentation measures being the most important variables across all three facets we explored. Interestingly, best-performing (ΔAICc < 2) models to perform equally well included only fragmentation, but not the forest area variables (Table 2). Functional and phylogenetic diversity were best-explained by the patch density variable (measured at the 1-km scale) and the edge density variable (measures at the 3-km scale), respectively (Fig. 3). The taxonomic diversity (i.e., richness) of forest birds did not respond appreciably to our predictor variables (Table 2). Most diversity facets were best predicted with variables measured at the 3-km scale (Fig. 3C-D), with the exception of phylogenetic diversity and functional diversity, where the best-fitting model also contained forest area and patch density respectively summarized at the 1-km scale (Table 2).

When averaging across the best-performing models per facet, we found for all birds that the best model had a positive relationship with edge density (3-km) for taxonomic diversity (Table 3, Fig. 3A). Our averaged model had a positive relationship with forest area and edge density for functional diversity, while phylogenetic diversity increases with lower forest area and higher edge density (Table 3, Fig. 3B). For forest birds, we found that best models predicted changes in functional and phylogenetic diversity, with a negative relation with patch density (1-km) and positive relation with edge density (3-km) respectively (Table 3, Fig. 3C, D).

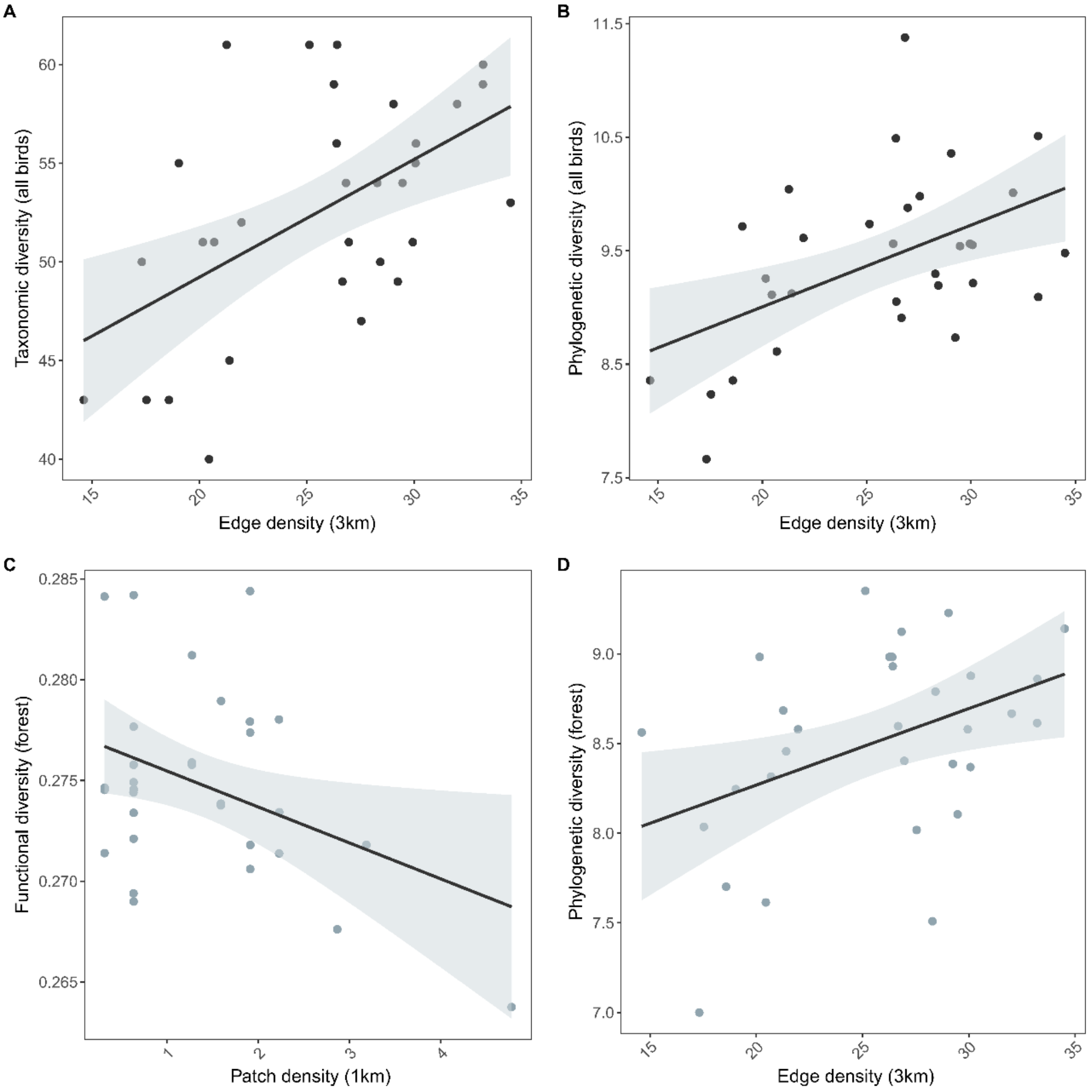


Fig. 3. Relationships of landscape predictors and diversity facets (taxonomic diversity, functional diversity and phylogenetic diversity) for the communities of all birds (A-B) and forest birds (C-D) in the Paraguayan Dry Chaco. Graphs show results of best and averaged models. All relationships shown are significant (p <0.05), shaded areas are 95% confidence intervals.

Table 2. Best-performing models (ΔAICc < 2) explaining the relationship between variables measuring forest area and forest fragmentation, for three facets of avian diversity. Two sets of models are shown: models explaining diversity in the communities of all birds and models explaining diversity in the community of forest birds only.

All birds	*Best performing model*	*AICc*	*ΔAICc*	*AICc w*	*p*
Taxonomic diversity	Edge density (3km)	198.213	0.000	0.465	0.017
Functional diversity	Forest area (3km) + Edge density (3km)	-221.955	0.000	0.339	
	Forest area (3km)	-220.351	-1.603	0.152	0.093
Phylogenetic diversity	Forest area (1km) + Edge density (3km)	64.5424	0.000	0.547	
Forest birds					
Taxonomic diversity	Edge density (3km)	183.797	0.000	0.399	0.044
	Null	185.561	1.763	0.165	
Functional diversity	Patch density (1km)	-242.918	0.000	0.371	0.033
Phylogenetic diversity	Edge density (3km)	49.8879	0.000	0.478	0.019

Table 3. Final, single best and averaged models explaining the taxonomic, functional and phylogenetic diversity of all birds and forest birds in the Paraguayan Dry Chaco.

All birds						*Forest birds*				
	Best or average		*Relative importance*	*Estimate*	*p*	*Best or average*		*Relative importance*	*Estimate*	*p*
Taxonomic diversity	Best	Edge density (3km)	-	0.0089	0.0173	Best	Edge density (3km)	-	0.0115	0.0448
							Null			
Functional diversity	Average	Forest area (3km)	1.00	0.000003	0.0562	Best	Patch density (1km)	-	-0.0011	0.03390
		Edge density (3km)	0.69	0.00043	0.0522					
Phylogenetic diversity	Average	Edge density (3km)	0.69	0.071987	0.00281	Best	Edge density (3km)	-	0.0349	0.01980
		Forest area (1km)	0.31	-0.00369	0.00769					

Discussion

Agricultural expansion is a key driver of biodiversity loss, particularly in the tropics. However, our understanding of how different aspects of agricultural expansion, particularly habitat loss and habitat fragmentation relate to biodiversity change remains weakly understood. This is particularly so for tropical dry forest, which are understudied, yet disappearing rapidly in many regions of the world. Using an unique field dataset, we provide here to our knowledge first assessment of the relative effects of habitat loss and habitat fragmentation on facets of avian biodiversity in the Paraguayan Chaco. Our study provided three main insights. First, we found that habitat loss and fragmentation affected different facets of avian diversity differently, with functional and phylogenetic diversity being most sensitive to changes in fragmentation, whereas taxonomic diversity was relatively unaffected by landscape change. This corroborates prior work stressing the need to assess land-use change impacts across multiple biodiversity facets (Laliberté et al. 2010; Flynn et al. 2011; Li et al. 2020). Second, we uncover considerable differences in the responses of the entire bird community compared to the responses of the forest bird community alone. Whereas habitat amount and fragmentation together helped to explained variation for the entire bird community, forest fragmentation alone explained diversity in forest birds. Given that many forest specialists are of conservation concern, this highlights how a focus on general diversity can miss biodiversity declines (Jetz et al. 2007; Harris and Pimm 2008; Nori et al. 2016). Third, we found a general increase in avian diversity with increasing landscape complexity (e.g., lower forest area, higher edge density) across diversity facets for all birds. This adds to a growing body of evidence suggesting that landscape transformations do not necessarily lead to overall diversity loss, but rather trigger turnover in community composition (Fletcher et al. 2018; Fahrig et al. 2019; Daskalova et al. 2020). Overall, our study contributes to a better understanding of the effects of habitat loss and habitat fragmentation in the Chaco, a global hotspot of deforestation and defaunation, and other tropical dry forests. Biodiversity monitoring and conservation planning should consider different facets of diversity, to understand how deforestation impacts on biodiversity and to avoid unwanted outcomes.

Our first main finding was that habitat amount and fragmentation affected the different facets of avian diversity differently, with functional and phylogenetic diversity being more sensitive to landscape transformation and specifically fragmentation than taxonomic diversity. Interestingly, in our case, habitat amount it self-did not explain changes in taxonomic diversity well, which contrasts from studies in other tropical forest

(Rurangwa et al. 2021), as well as from the Chaco (Romero-Muñoz et al. 2021; Semper-Pascual et al. 2021). While this finding warrants further investigation, possible explanations for these diverse findings include (1) potential non-linear relationships (Legrand et al. 2017), especially if different sections of the diversity gradients are covered by different studies (Allouche et al. 2012; Bełcik et al. 2020), (2) time-delayed responses, where bird community might not responded yet to habitat fragmentation (Semper-Pascual et al. 2021), which is plausible given the fast speed at which landscape change has taken place in Paraguay recently(Baumann et al. 2022), and (3) sustained connectivity of forest patches through elements such as forest strips in the Paraguayan Chaco (Nord and Forslund 2015; de la Sancha et al. 2021).

In our study, functional and phylogenetic diversity for the entire community of birds were better explained by landscape variables (Table 2). This highlights the need to move beyond assessing taxonomic richness only when seeking to understand the importance of fragmentation (Fletcher et al. 2018; Fahrig et al. 2019). Several studies from temperate and rainforest regions have recently suggested that functional and phylogenetic diversity should be less responsive to landscape change than taxonomic diversity, due to redundancy of functions within bird communities (Bełcik et al. 2020; Matuoka et al. 2020; Rurangwa et al. 2021). This view is not supported by our study, where functional and phylogenetic diversity were more clearly affected by landscape change, in line with work on mammals in the Chaco (Romero-Muñoz et al. 2021). Interestingly, functional diversity was equally affected by fragmentation and habitat amount, but we highlight that our best model also included habitat amount (Table 2). Thus, the positive contribution of fragmentation might depends on enough habitat being available in the landscape (Cadotte et al. 2011). Finally, the positive relationship we find between fragmentation and phylogenetic diversity (Fig. 3B) can be explained by species more close related to each other sharing similar habitats (Flynn et al. 2009), as well as species from younger lineages or recently diversifying clades being more generalist and therefore able to colonize areas dominated by agriculture (Frishkoff et al. 2014).

Our second main finding was that there are considerable differences in the responses of the entire bird community versus the responses of forest bird community to landscape change. For forest birds, fragmentation decrease diversity, especially functional diversity. This can be explained by four main factors. First, environmental filters likely act on functional traits, with land-use change likely impacting species with specific traits (e.g. dispersal, fecundity, colonization, and stress tolerance) most negatively (Flynn et al. 2009; Mayfield et al. 2010). Second, given the relative homogeneity of our study region, there is likely have low superposition of species niches, meaning that the loss of individual, key species lower the functionally diversity of a community strongly (Wiens et al. 2010). Overall, our study thus points to the risks of analyzing the impacts of land-use change on biodiversity generally, as this communities that contain generalist species (winners) and specialist species (losers, forest species in our case), might mask declines in those species most relevant from a conservation perspective (Wiens et al. 2010; Legrand et al. 2017). This might be particularly the case in situation of low functional redundancy, often associated with higher phylogenetic diversity (Wiens et al. 2010; Cadotte et al. 2011), which appears to be the case for our study region. For the Paraguayan Chaco, forest birds might be a useful focal taxa for conservation planning.

Our third main finding is a general increase in the diversity of avian community with increasing landscape complexity (e.g., lower forest area, higher edge density) across facets of diversity. This is in line with views that spatial heterogeneity does not necessarily lead to diversity loss, but rather triggers turnover in community composition and can sometimes lead to diversity increases (Fahrig et al. 2019). As we highlight above, this should not be interpreted as habitat loss and fragmentation not being of conservation concern – the community of forest birds suffers from landscape change, and most species of conservation concern are found in this group of species (i.e., *Strix chacoensis and Dryocopus schulzii* are classified as threatened by IUCN in our community). This increase in the diversity of all birds we find is, as has been extensively discussed in the literature, likely driven by generalist species benefitting from landscape heterogeneity and replacing other species, as well as other compensatory effects (Allouche et al. 2012; Fletcher et al. 2018). Importantly, analyzing functional diversity can uncover the 'hidden' and negative effect of habitat fragmentation (Table 3), helping to resolve the debate around the role of fragmentation that has focused mainly on taxonomic diversity so far (Fletcher et al. 2018; Fahrig et al. 2019).

Our study relied on a large sample of primary field data from the Paraguayan Dry Chaco, gathered using acoustic recorders, which made it possible to monitor bird communities in multiples sites at the same time. This method has been shown to be robust in terms of detectability of a large pool of species including nocturnal and diurnal birds (Machado et al. 2017; Owen et al. 2020), allowing us to detect rare birds often missed in other studies in the Chaco (Semper-Pascual et al. 2018). This mean, the method allowed a wider monitoring in space and time compare with active monitoring methods. Still, some limitations should be mentioned. We limited our sampling to the dry season, and the bird community will changed during the wet season, when more migratory birds will be present (Gonçalves et al. 2017). Second, we excluded smaller forest patches from the landscape metrics, although such patches could be important stepping stones in the wider landscape. Third, we used a range for fragmentation measures but did not explicitly account for connectivity, given the mobility of our target taxa, but landscape connectivity might still influence birds' responses (Mastrangelo and Gavin 2014; Torres et al. 2014; Macchi et al. 2015). Fourth, we did not include forest stand age and disturbance history, although this may play a role in determining diversity (Bełcik et al. 2020; Semper-Pascual et al. 2021). Fifth, we focused on forest and pasture areas only, but with an increasing replacement of pastures by cropland, analyzing the response of birds to this land-use intensification would be beneficial. Finally, we focused here on landscape structure, but climate variables and vegetation condition could be important as well (Sitters et al. 2016; Zelaya et al. 2022).

Our study adds to a growing body of literature suggesting that landscape change does not necessarily lead to an overall loss in diversity, but rather triggers a turnover in community composition. Likewise, our study cautions that much biodiversity change due to land-use change will go unnoticed when not assessing multiple facets of biodiversity, and when focusing on the entire community of species. In the Dry Chaco and likely many other dry forests undergoing similar dynamics, forest birds are particularly threatened (Matuoka et al. 2020) and of great conservation concern, as functionally unique species are lost (Sekercioglu 2006). Larger areas of dry forest are still remaining in the central and northern of the Paraguayan Dry Chaco, where swift and landscape-scale conservation planning is needed to avoid major biodiversity losses that characterize other areas of Chaco. We recommend continuous monitoring of forest birds and their functional diversity to understanding threats to biodiversity due to land-use change, to devise monitoring for an early warning system and to carry out conservation planning and prioritizing to avoid wider biodiversity erosion (Rapacciuolo et al. 2019).

Acknowledgements

We are grateful to the Brazilian Ministry of Education (CAPES) for a PhD scholarship to RC. We thank the German Academic Exchange (DAAD-CAPES) and Humboldt-Universität zu Berlin for hosting RC during a research stay. We also thank the Rufford

Small Grants Foundation (#28259-1) and the Graduate Program in Ecology, University of Brasilia (CAPES/PROEX) for financial support for purchasing sound recorder and the fieldwork. We are indebted to Hugo del Castillo and Lucas Cañete for assistance in the fieldwork and all landowners for granting access to their properties.

References

Allouche O, Kalyuzhny M, Moreno-Rueda G, et al (2012) Area-heterogeneity tradeoff and the diversity of ecological communities. Proc Natl Acad Sci U S A 109:17495–17500. https://doi.org/10.1073/pnas.1208652109

Barton K (2022) MuMIn: Multi-Model Inference. In: R Packag. Version 1.46.0. https://cran.r-project.org/package=MuMIn

Baumann M, Gasparri I, Piquer-Rodríguez M, et al (2017) Carbon emissions from agricultural expansion and intensification in the Chaco. Glob Chang Biol 23:1902–1916. https://doi.org/10.1111/gcb.13521

Baumann M, Gasparri NI, Buchadas A, et al (2022) Frontier metrics for a process-based understanding of deforestation dynamics. Environ Res Lett. https://doi.org/10.1088/1748-9326/ac8b9a

Bełcik M, Lenda M, Amano T, Skórka P (2020) Different response of the taxonomic, phylogenetic and functional diversity of birds to forest fragmentation. Sci Rep 10:1–11. https://doi.org/10.1038/s41598-020-76917-2

Bierregaard, RO, Lovejoy TE, Kapos V, Hutchings RW (1992) The Biological Dynamics of Tropical Rainforest Fragments. Bioscience 42:859–866. https://doi.org/10.2307/1312085

Buchadas A, Baumann M, Meyfroidt P, Kuemmerle T (2022) Uncovering major types of deforestation frontiers across the world’s tropical dry woodlands. Nat Sustain. https://doi.org/10.1038/s41893-022-00886-9

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behav Ecol Sociobiol 65:23–35. https://doi.org/10.1007/s00265-010-1029-6

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: Functional diversity and the maintenance of ecological processes and services. J Appl Ecol 48:1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Calcagno V, de Mazancourt C (2010) glmulti: An R package for easy automated model selection with (generalized) linear models. J Stat Softw 34:29. https://doi.org/10.18637/jss.v034.i12

Center for Conservation Bioacoustics (2019) Raven Pro: Interactive Sound Analysis Software [Computer software]

Cernansky R (2017) The biodiversity revolution. Nature 546:22–24. https://doi.org/10.1038/546022a

Dardanelli S, Nores ML, Nores M (2006) Minimum area requirements of breeding birds in fragmented woodland of Central Argentina. Divers Distrib 12:687–693. https://doi.org/10.1111/j.1472-4642.2006.00266.x

Daskalova GN, Myers-Smith IH, Bjorkman AD, et al (2020) Landscape-scale forest loss as a catalyst of population and biodiversity change. Science (80-) 368:1341–1347. https://doi.org/10.1126/science.aba1289

Davis KF, Koo HI, Dell'Angelo J, et al (2020) Tropical forest loss enhanced by large-scale land acquisitions. Nat Geosci 13:482–488. https://doi.org/10.1038/s41561-020-0592-3

de la Sancha NU, Boyle SA, McIntyre NE, et al (2021) The disappearing Dry Chaco, one of the last dry forest systems on earth. Landsc Ecol 36:2997–3012. https://doi.org/10.1007/s10980-021-01291-x

Dirzo R, Young HS, Galetti M, et al (2014) Defaunation in the Anthropocene. Science (80-) 345:401–406. https://doi.org/10.1126/science.1251817

Ericson PGP, Anderson CL, Britton T, et al (2006) Diversification of Neoaves: Integration of molecular sequence data and fossils. Biol Lett 2:543–547. https://doi.org/10.1098/rsbl.2006.0523

Escribano-Avila G, Cervera L, Ordóñez-Delgado L, et al (2017) Biodiversity patterns and ecological processes in Neotropical dry forest: the need to connect research and management for long-term conservation. Neotrop Biodivers 3:107–116. https://doi.org/10.1080/23766808.2017.1298495

Fahrig L (2003) Effects of Habitat Fragmentation on Biodiversity. Annu Rev Ecol Evol Syst 34:487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fahrig L (2013) Rethinking patch size and isolation effects: The habitat amount hypothesis. J Biogeogr 40:1649–1663. https://doi.org/10.1111/jbi.12130

Fahrig L, Arroyo-Rodríguez V, Bennett JR, et al (2019) Is habitat fragmentation bad for biodiversity? Biol Conserv 230:179–186. https://doi.org/10.1016/j.biocon.2018.12.026

Faith DP (1992) Conservation evaluation and phylogenetic diversity. Biol Conserv 61:1–10. https://doi.org/10.1016/0006-3207(92)91201-3

Fletcher RJ, Didham RK, Banks-Leite C, et al (2018) Is habitat fragmentation good for biodiversity? Biol Conserv 226:9–15. https://doi.org/10.1016/j.biocon.2018.07.022

Flynn DFB, Gogol-Prokurat M, Nogeire T, et al (2009) Loss of functional diversity under land use intensification across multiple taxa. Ecol Lett 12:22–33. https://doi.org/10.1111/j.1461-0248.2008.01255.x

Flynn DFB, Mirotchnick N, Jain M, et al (2011) Functional and phylogenetic diversity as predictors of biodiversity- Ecosystem-function relationships. Ecology 92:1573–1581. https://doi.org/10.1890/10-1245.1

Foley JA, DeFries R, Asner GP, et al (2005) Global consequences of land use. Science (80-.). 309:570–574

Franco-Solís A, Montanía C V. (2021) Dynamics of deforestation worldwide: A structural decomposition analysis of agricultural land use in South America. Land use policy 109:105619. https://doi.org/10.1016/j.landusepol.2021.105619

Frishkoff LO, Karp DS, M'Gonigle LK, et al (2014) Loss of avian phylogenetic diversity in neotropical agricultural systems. Science (80-) 345:1343–1346. https://doi.org/10.1126/science.1254610

Gonçalves GSR, Cerqueira PV, Brasil LS, Santos MPD (2017) The role of climate and environmental variables in structuring bird assemblages in the Seasonally Dry Tropical Forests (SDTFs). PLoS One 12:1–16. https://doi.org/10.1371/journal.pone.0176066

Gregory RD, Van Strien A, Vorisek P, et al (2005) Developing indicators for European birds. Philos Trans R Soc B Biol Sci 360:269–288. https://doi.org/10.1098/rstb.2004.1602

Haddad NM, Brudvig LA, Clobert J, et al (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:1–9. https://doi.org/10.1126/sciadv.1500052

Hansen MC, Potapov P V, Moore R, et al (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850–3. https://doi.org/10.1126/science.1244693

Hanski I (1998) Metapopulation dynamics. Nature 396:41–49. https://doi.org/10.1038/23876

Harris G, Pimm SL (2008) Range size and extinction risk in forest birds. Conserv Biol 22:163–171. https://doi.org/10.1111/j.1523-1739.2007.00798.x

Hill AP, Prince P, Piña Covarrubias E, et al (2018) AudioMoth: Evaluation of a smart open acoustic device for monitoring biodiversity and the environment. Methods Ecol Evol 9:1199–1211. https://doi.org/10.1111/2041-210X.12955

Jetz W, Thomas GH, Joy JB, et al (2012) The global diversity of birds in space and time. Nature 491:444–448. https://doi.org/10.1038/nature11631

Jetz W, Wilcove DS, Dobson AP (2007) Projected impacts of climate and land-use change on the global diversity of birds. PLoS Biol 5:1211–1219. https://doi.org/10.1371/journal.pbio.0050157

Johnson CN, Balmford A, Brook BW, et al (2017) Biodiversity losses and conservation responses in the Anthropocene. Science (80-) 356:270–275. https://doi.org/10.1126/science.aam9317

Kembel SW, Cowan PD, Helmus MR, et al (2010) Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kuemmerle T, Baldi G, Camino M, et al (2017) Forest conservation : Remember Gran Chaco Forest conservation : Humans ' handprints. Science (80-) 355:465–467

Laliberte E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305

Laliberté E, Wells JA, Declerck F, et al (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecol Lett 13:76–86. https://doi.org/10.1111/j.1461-0248.2009.01403.x

Lambin EF, Meyfroidt P (2011) Global land use change, economic globalization, and the looming land scarcity. Proc Natl Acad Sci U S A 108:3465–3472. https://doi.org/10.1073/pnas.1100480108

Laurance WF, Sayer J, Cassman KG (2014) Agricultural expansion and its impacts on tropical nature. Trends Ecol Evol 29:107–116. https://doi.org/10.1016/j.tree.2013.12.001

Legrand D, Cote J, Fronhofer EA, et al (2017) Eco-evolutionary dynamics in fragmented landscapes. Ecography (Cop) 40:9–25. https://doi.org/10.1111/ecog.02537

Li D, Olden JD, Lockwood JL, et al (2020) Changes in taxonomic and phylogenetic diversity in the Anthropocene: Changes in biodiversity. Proc R Soc B Biol Sci 287:. https://doi.org/10.1098/rspb.2020.0777rspb20200777

Macchi L, Decarre J, Goijman AP, et al (2020) Trade-offs between biodiversity and agriculture are moving targets in dynamic landscapes. J Appl Ecol 1–10. https://doi.org/10.1111/1365-2664.13699

Macchi L, Grau HR, Phalan B (2015) Agricultural production and bird conservation in complex landscapes of the dry Chaco. J Land Use Sci 11:188–202. https://doi.org/10.1080/1747423X.2015.1057244

Machado RB, Aguiar L, Jones G (2017) Do acoustic indices reflect the characteristics of bird communities in the savannas of Central Brazil? Landsc Urban Plan 162:36–43. https://doi.org/10.1016/j.landurbplan.2017.01.014

Martin LJ, Blossey B, Ellis E (2012) Mapping where ecologists work: Biases in the global distribution of terrestrial ecological observations. Front Ecol Environ 10:195–201. https://doi.org/10.1890/110154

Mastrangelo ME, Gavin MC (2014) Impacts of agricultural intensification on avian richness at multiple scales in Dry Chaco forests. Biol Conserv 179:63–71. https://doi.org/10.1016/j.biocon.2014.08.020

Matuoka MA, Benchimol M, Almeida-Rocha JM de, Morante-Filho JC (2020) Effects of anthropogenic disturbances on bird functional diversity: A global meta-analysis. Ecol Indic 116:106471. https://doi.org/10.1016/j.ecolind.2020.106471

Mayfield MM, Bonser SP, Morgan JW, et al (2010) What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. Glob Ecol Biogeogr 19:423–431. https://doi.org/10.1111/j.1466-8238.2010.00532.x

Mayorga I, Bichier P, Philpott SM (2020) Local and landscape drivers of bird abundance, species richness, and trait composition in urban agroecosystems. Urban Ecosyst 23:495–505. https://doi.org/10.1007/s11252-020-00934-2

McGarigal K (2014) Landscape Pattern Metrics. Wiley StatsRef Stat Ref Online 1–13. https://doi.org/10.1002/9781118445112.stat07723

Mereles MF, Rodas O (2014) Assessment of rates of deforestation classes in the Paraguayan Chaco (Great South American Chaco) with comments on the vulnerability of forests fragments to climate change. Clim Change 127:55–71. https://doi.org/10.1007/s10584-014-1256-3

Milán MJ, González E (2022) Beef–cattle ranching in the Paraguayan Chaco: typological approach to a livestock frontier. Environ Dev Sustain. https://doi.org/10.1007/s10668-022-02261-2

Miles L, Newton AC, DeFries RS, et al (2006) A global overview of the conservation status of tropical dry forests. J Biogeogr 33:491–505. https://doi.org/10.1111/j.1365-2699.2005.01424.x

Miller-Rushing AJ, Primack RB, Devictor V, et al (2019) How does habitat fragmentation affect biodiversity? A controversial question at the core of conservation biology. Biol Conserv 232:271–273. https://doi.org/10.1016/j.biocon.2018.12.029

Navarro G, Molina JA, Vega S (2011) Soil factors determining the change in forests between dry and wet Chacos. Flora Morphol Distrib Funct Ecol Plants 206:136–143. https://doi.org/10.1016/j.flora.2010.09.002

Nord M, Forslund P (2015) Environmental gradients explain species richness and community composition of coastal breeding birds in the baltic sea. PLoS One 10:1–16. https://doi.org/10.1371/journal.pone.0118455

Nori J, Torres R, Lescano JN, et al (2016) Protected areas and spatial conservation priorities for endemic vertebrates of the Gran Chaco, one of the most threatened ecoregions of the world. Divers Distrib 22:1212–1219. https://doi.org/10.1111/ddi.12497

Owen KC, Melin AD, Campos FA, et al (2020) Bioacoustic analyses reveal that bird communities recover with forest succession in tropical dry forests. Avian Conserv Ecol 15:1–20. https://doi.org/10.5751/ACE-01615-150125

Parker III TA, Stotz DF, Fitzpatrick JW (1996) Ecological and Distributional Databases for Neotropical Birds. University of Chicago Press, Chicago

Pavoine S, Vallet J, Dufour A-B, et al (2009) On the challenge of treating various types of variables: application for improving the measurement of functional diversity. Oikos 118:391–402. https://doi.org/10.1111/j.1600-0706.2009.16668.x

Pendrill F, Gardner TA, Meyfroidt P, et al (2022) Disentangling the numbers behind agriculture-driven tropical deforestation. Science (80-) 377:. https://doi.org/10.1126/science.abm9267

Pennington RT, Lehmann CER, Rowland LM (2018) Tropical savannas and dry forests. Curr Biol 28:R541–R545. https://doi.org/10.1016/j.cub.2018.03.014

Pennington TR, Prado DE, Pendry CA (2000) Neotropical seasonally dry forests and Quaternary vegetation changes. J Biogeogr 27:261–273. https://doi.org/10.1046/j.1365-2699.2000.00397.x

Pérez-Granados C, Traba J (2021) Estimating bird density using passive acoustic monitoring: a review of methods and suggestions for further research. Ibis (Lond. 1859). 163:765–783

Pfeifer M, Lefebvre V, Peres CA, et al (2017) Creation of forest edges has a global impact on forest vertebrates. Nature 551:187–191. https://doi.org/10.1038/nature24457

Pollock LJ, O'Connor LMJ, Mokany K, et al (2020) Protecting Biodiversity (in All Its Complexity): New Models and Methods. Trends Ecol Evol 35:1119–1128. https://doi.org/10.1016/j.tree.2020.08.015

Portillo-Quintero CA, Sánchez-Azofeifa GA (2010) Extent and conservation of tropical dry forests in the Americas. Biol Conserv 143:144–155. https://doi.org/10.1016/j.biocon.2009.09.020

R Core Team (2021) R: A language and environment for statistical computing. In: R Found. Stat. Comput. http://www.r-project.org/

Rapacciuolo G, Graham CH, Marin J, et al (2019) Species diversity as a surrogate for conservation of phylogenetic and functional diversity in terrestrial vertebrates across the Americas. Nat Ecol Evol 3:53–61. https://doi.org/10.1038/s41559-018-0744-7

Revell LJ (2012) phytools: An R package for phylogenetic comparative biology (and other things). Methods Ecol Evol 3:217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Romero-Muñoz A, Fandos G, Benítez-López A, Kuemmerle T (2021) Habitat destruction and overexploitation drive widespread declines in all facets of mammalian diversity in the Gran Chaco. Glob Chang Biol 27:755–767. https://doi.org/10.1111/gcb.15418

Roque FDO, Menezes JFS, Northfield T, et al (2018) Warning signals of biodiversity collapse across gradients of tropical forest loss. Sci Rep 8:1–7. https://doi.org/10.1038/s41598-018-19985-9

Rurangwa ML, Aguirre-Gutiérrez J, Matthews TJ, et al (2021) Effects of land-use change on avian taxonomic, functional and phylogenetic diversity in a tropical montane rainforest. Divers Distrib 27:1732–1746. https://doi.org/10.1111/ddi.13364

Sekercioglu CH (2006) Increasing awareness of avian ecological function. Trends Ecol Evol 21:464–471. https://doi.org/10.1016/j.tree.2006.05.007

Sekercioglu CH (2012) Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. J Ornithol 153:153–161. https://doi.org/10.1007/s10336-012-0869-4

Semper-Pascual A, Burton C, Baumann M, et al (2021) How do habitat amount and habitat fragmentation drive time-delayed responses of biodiversity to land-use change? Proc R Soc B Biol Sci 288:. https://doi.org/10.1098/rspb.2020.2466

Semper-Pascual A, Macchi L, Sabatini FM, et al (2018) Mapping extinction debt highlights conservation opportunities for birds and mammals in the South American Chaco. J Appl Ecol 55:1218–1229. https://doi.org/10.1111/1365-2664.13074

Sitters H, York A, Swan M, et al (2016) Opposing responses of bird functional diversity to vegetation structural diversity in wet and dry forest. PLoS One 11:1–18. https://doi.org/10.1371/journal.pone.0164917

Siyum ZG (2020) Tropical dry forest dynamics in the context of climate change: syntheses of drivers, gaps, and management perspectives. Ecol Process 9:.

https://doi.org/10.1186/s13717-020-00229-6

Sodhi NS, Smith KG (2007) Conservation of tropical birds: Mission possible? J Ornithol 148:305–309. https://doi.org/10.1007/s10336-007-0180-y

Song X-P, Hansen MC, Stehman S V., et al (2018) Global land change from 1982 to 2016. Nature. https://doi.org/10.1038/s41586-018-0411-9

Sugai LSM, Silva TSF, Ribeiro JW, Llusia D (2019) Terrestrial Passive Acoustic Monitoring: Review and Perspectives. Bioscience 69:5–11. https://doi.org/10.1093/biosci/biy147

Tilman D, Clark M, Williams DR, et al (2017) Future threats to biodiversity and pathways to their prevention. Nature 546:73–81. https://doi.org/10.1038/nature22900

Tobias JA, Sheard C, Pigot AL, et al (2022) AVONET: morphological, ecological and geographical data for all birds. Ecol Lett 25:581–597. https://doi.org/10.1111/ele.13898

Torres R, Gasparri NI, Blendinger PG, Grau HR (2014) Land-use and land-cover effects on regional biodiversity distribution in a subtropical dry forest: A hierarchical integrative multi-taxa study. Reg Environ Chang 14:1549–1561. https://doi.org/10.1007/s10113-014-0604-1

Trimble MJ, van Aarde RJ (2012) Geographical and taxonomic biases in research on biodiversity in human-modified landscapes. Ecosphere 3:art119. https://doi.org/10.1890/es12-00299.1

Vallejos M, Volante JN, Mosciaro MJ, et al (2015) Transformation dynamics of the natural cover in the Dry Chaco ecoregion: A plot level geo-database from 1976 to 2012. J Arid Environ 123:3–11. https://doi.org/10.1016/j.jaridenv.2014.11.009

Vandewalle M, de Bello F, Berg MP, et al (2010) Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. Biodivers Conserv 19:2921–2947. https://doi.org/10.1007/s10531-010-9798-9

Werneck FP (2011) The diversification of eastern South American open vegetation biomes: Historical biogeography and perspectives. Quat Sci Rev 30:1630–1648. https://doi.org/10.1016/j.quascirev.2011.03.009

Wiens JA (1999) Habitat fragmentation: island v landscape perspectives on bird conservation

Wiens JJ, Ackerly DD, Allen AP, et al (2010) Niche conservatism as an emerging principle in ecology and conservation biology. Ecol Lett 13:1310–1324. https://doi.org/10.1111/j.1461-0248.2010.01515.x

Zelaya P V., Blendinger PG, Palacio FX, et al (2022) Above-ground biomass and high temperatures are more important than productivity for the spatial pattern of bird richness in Subtropical Dry forests of Argentina. Community Ecol 23:41–54. https://doi.org/10.1007/s42974-021-00071-6

Supporting Information for:

Impacts of habitat loss and habitat fragmentation on multiple facets of avian diversity in a global deforestation hotspot

Fig. A1. Correlation matrix for the predictor variables candidates used in our models: forest area (ca), edge density (ed), number of patches (np), patch density (pd), total edge (te) and pasture (pas).

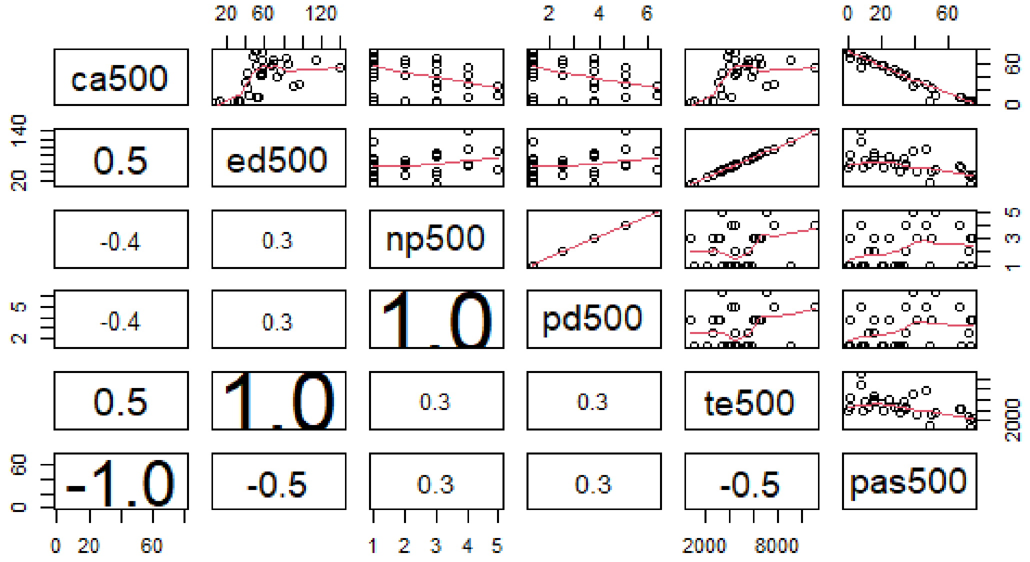


Fig. A2. Bivariate models showed correlation of forest area at different scales (0.5-km, 1-km, 3-km) and diversity facets (taxonomic diversity, functional diversity and phylogenetic diversity) for the communities of all birds (black points) and forest birds (gray points) in the Paraguayan Dry Chaco

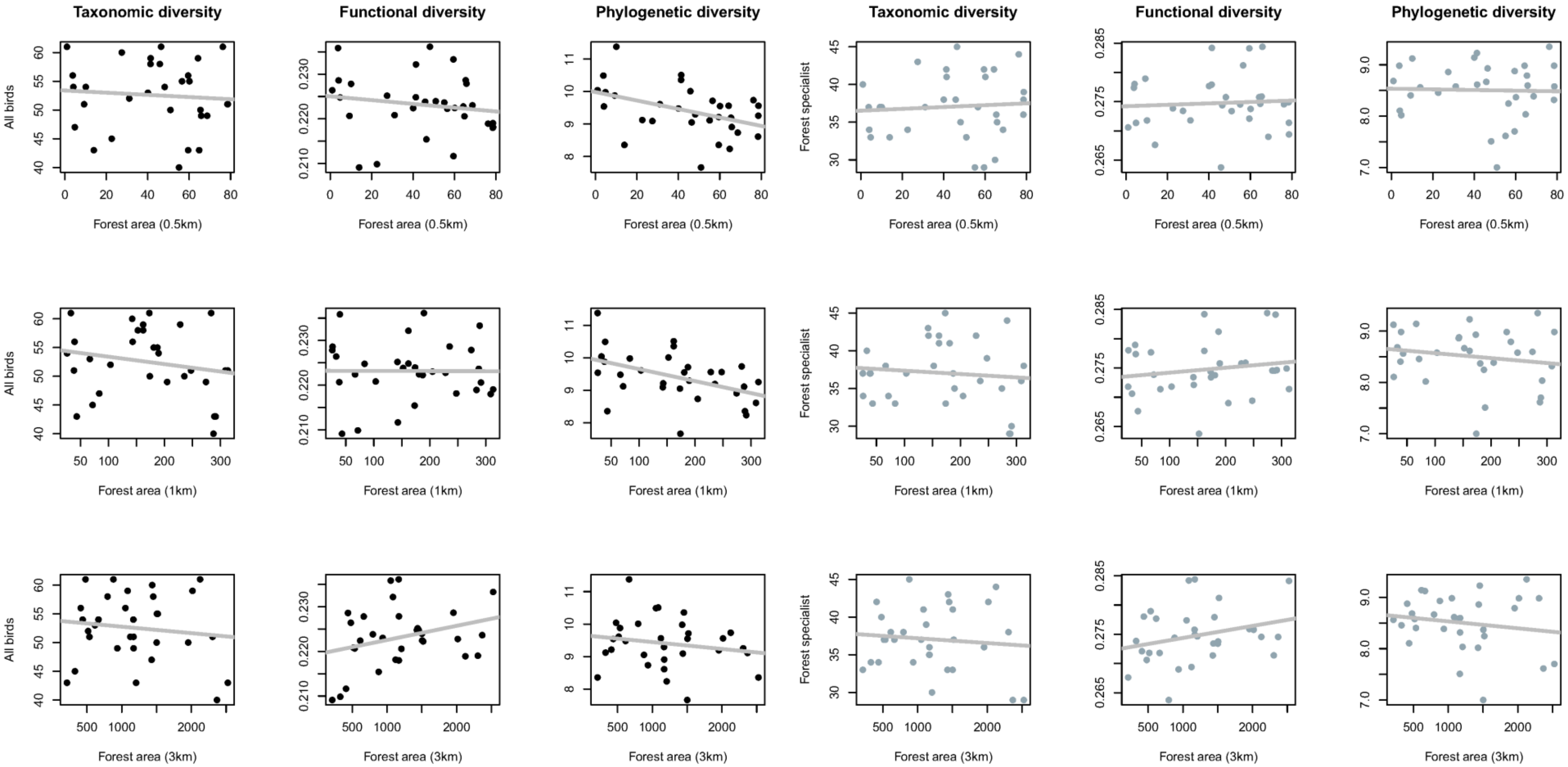


Fig. A3. Bivariate models showed correlation of patch density at different scales (0.5-km, 1-km, 3-km) and diversity facets (taxonomic diversity, functional diversity and phylogenetic diversity) for the communities of all birds (black points) and forest birds (gray points) in the Paraguayan Dry Chaco.

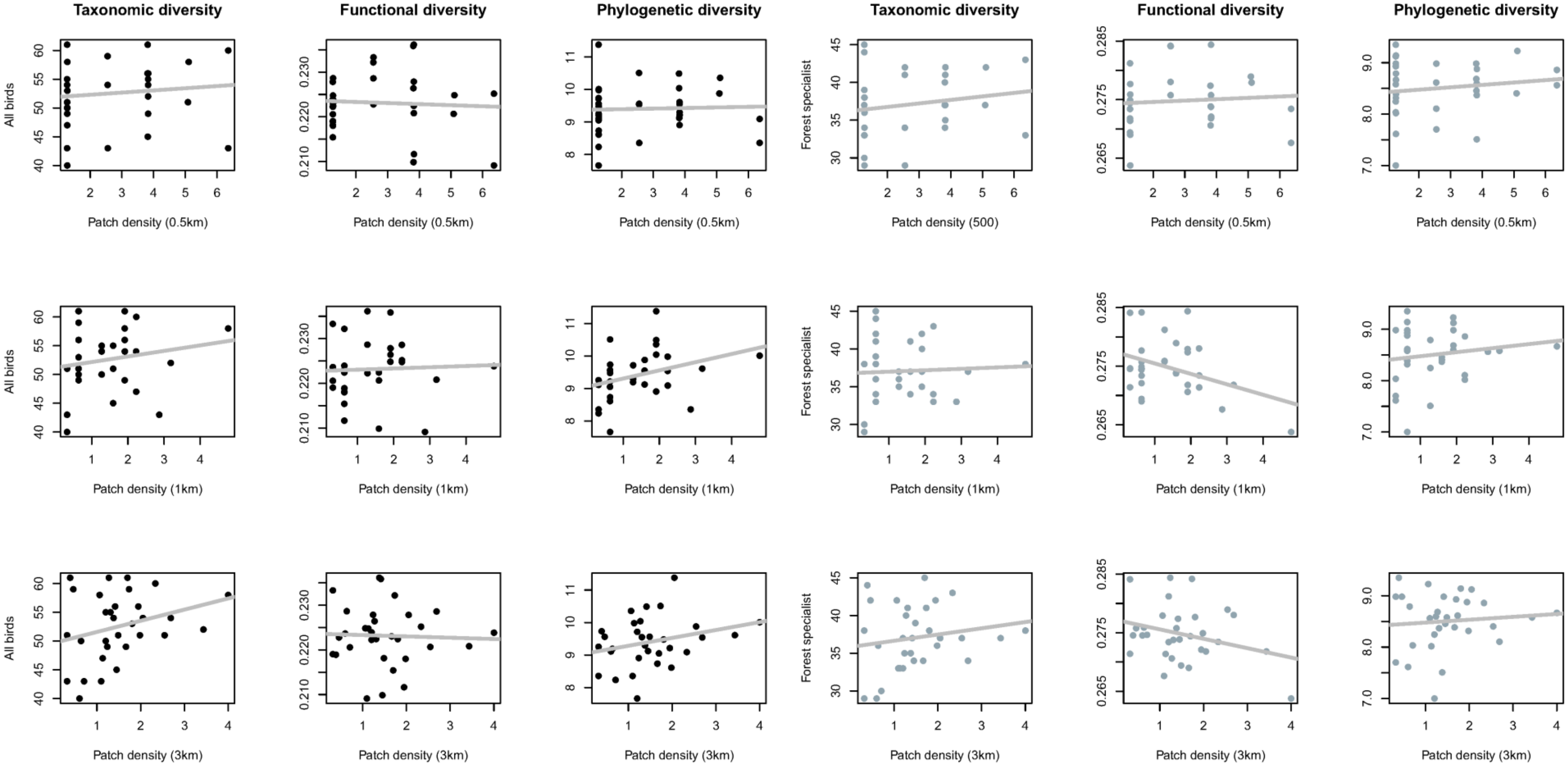


Fig. A4. Bivariate models showed correlation of edge density at different scales (0.5-km, 1-km, 3-km) and diversity facets (taxonomic diversity, functional diversity and phylogenetic diversity) for the communities of all birds (black points) and forest birds (gray points) in the Paraguayan Dry Chaco.

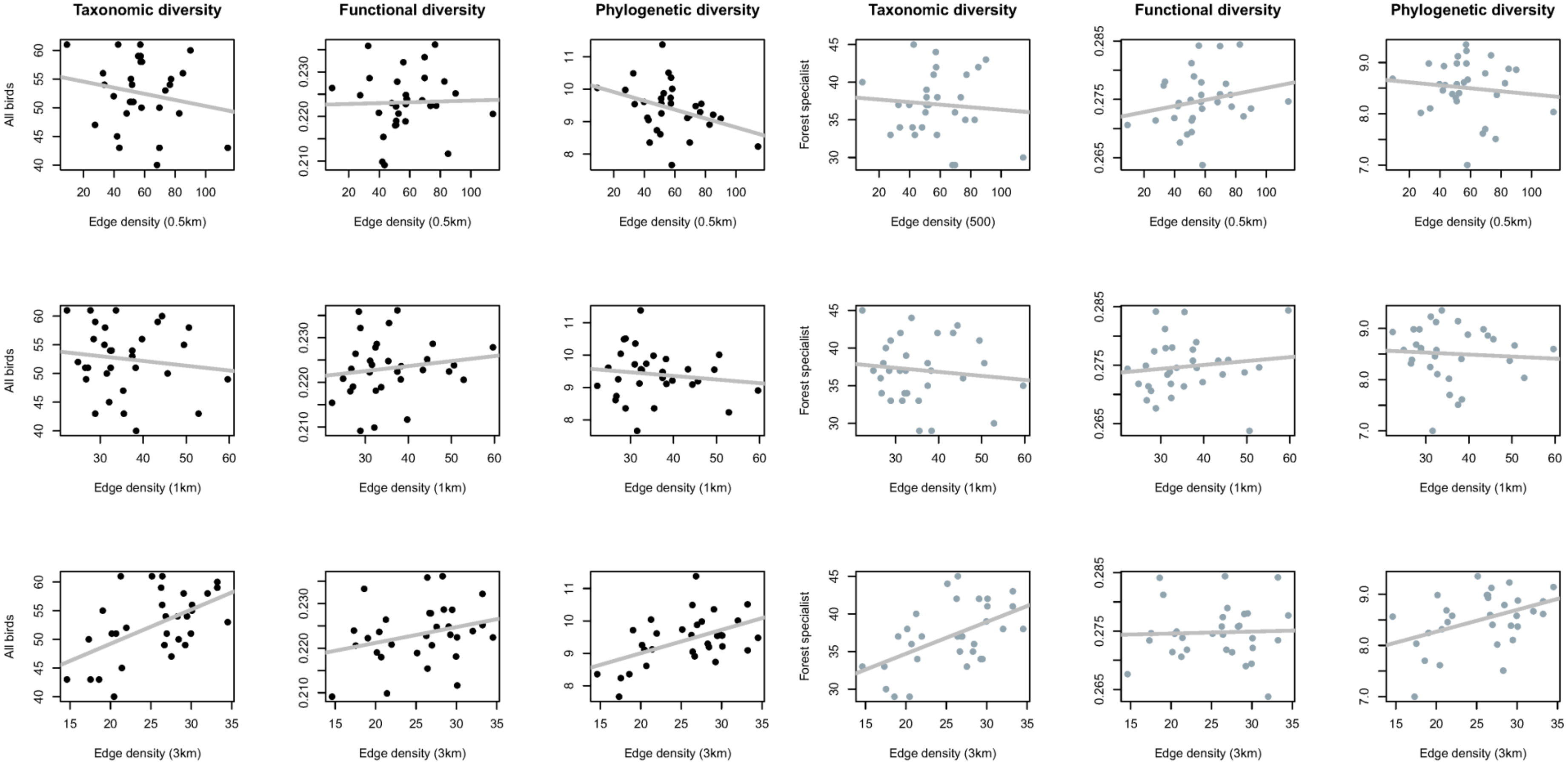


Fig. A5. Cluster dendrogram resulted from functional diversity analyses for all birds

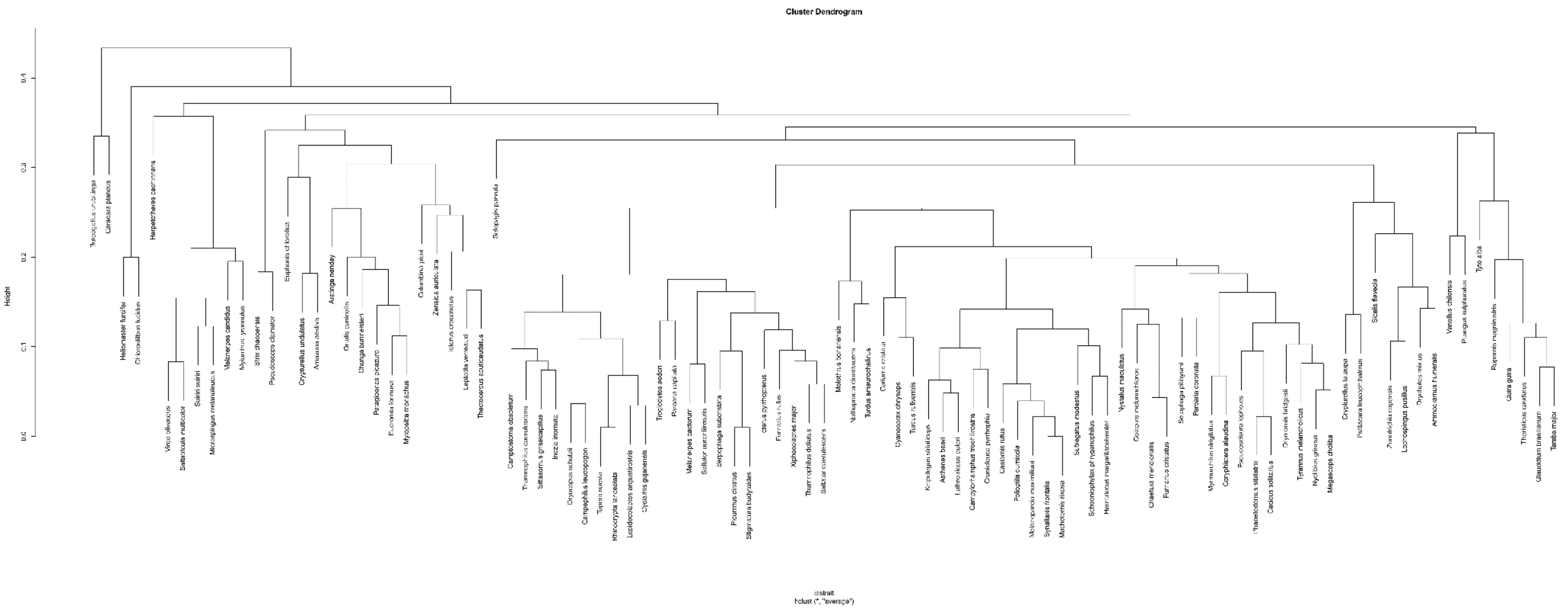


Table S1. Species trait compilation to generate the functional diversity (FD) metric: Diet, foraging stratum and body mass (geometric mean of average values provided for both sexes) were determined by the literature following Wilman et al. (2014). Diet traits were divided in PlantSeed, FruiNect, Omnivore and Invertebrate. Foraging stratum traits were (1) ground, (2) understory, (3) mid-to-high levels, (4) canopy, and (5) aerial. Diet and foraging stratum were based on estimated percentage usage of each category. Forest specialist and generalist birds were categorized as (G) generalist birds frequently occurring in other types of habitats, and (F) forest specialist restricted to forest, and strongly avoiding other types of habitats, following Dardanelli et al (2006), Semper-Pascual et al. (2018), Parker et al. (1996) and distribution maps on Birds of the world (https://birdsoftheworld.org/).

Species	Energetic level (diet)	Forest stratum	Body mass(g)	Forest/generalist
Eudromia formosa	PlantSeed	Ground	772.93	F
Crypturellus undulatus	FruiNect	Ground	564.42	F
Crypturellus tataupa	Omnivore	Ground-Understory	218.8	F
Nothoprocta cinerascens	Invertebrate	Ground-Understory	523.89	F
Ortalis canicollis	Omnivore	Ground-Midhigh-Canopy	539	F
Patagioenas picazuro	PlantSeed	Ground-Understory-Midhigh	279	G
Leptotila verreauxi	PlantSeed	Ground	146.88	G
Zenaida auriculata	PlantSeed	Ground-Understory-Midhigh-Canopy	110.2	G
Columbina picui	PlantSeed	Ground	47	G
Guira guira	VertFishScav	Ground-Understory-Midhigh	141	G
Tapera naevia	Invertebrate	Ground-Understory-Midhigh	48.42	G
Nyctibius griseus	Invertebrate	Midhigh-Aerial	172.04	F
Setopagis parvula	Invertebrate	Understory-Midhigh	37	G
Chaetura meridionalis	Invertebrate	Aerial	22.2	G
Heliomaster furcifer	FruiNect	Understory-Midhigh	5.4	F
Chlorostilbon lucidus	FruiNect	Midhigh	3.5	G
Vanellus chilensis	Invertebrate	Ground	327	G
Theristicus caudatus	Invertebrate	Ground	1726	G
Buteogallus urubitinga	VertFishScav	Ground-Canopy	1152.87	F
Rupornis magnirostris	VertFishScav	Ground-Understory	269	G
Tyto alba	VertFishScav	Ground-Understory	403.32	F
Megascops choliba	Invertebrate	Ground-Understory	132	F
Strix chacoensis	VertFishScav	Ground-Understory	330	F
Glaucidium brasilianum	Invertebrate	Ground-Understory	75.1	F
Pseudoscops clamator	VertFishScav	Ground-Understory	443.28	F
Nystalus maculatus	Invertebrate	Ground-Understory	42	F
Picumnus cirratus	Invertebrate	Understory-Midhigh	10.2	F
Melanerpes candidus	FruiNect	Understory-Midhigh	108	G
Melanerpes cactorum	Omnivore	Midhigh-Canopy	34.94	F

Dryocopus schulzii	Invertebrate	Midhigh-Canopy	200	F
Dryobates mixtus	Omnivore	Understory-Midhigh	28.74	F
Campephilus leucopogon	Invertebrate	Understory-Midhigh-Canopy	249	F
Colaptes melanochloros	Invertebrate	Understory-Midhigh	127.27	G
Cariama cristata	Invertebrate	Ground-Understory	1400	G
Chunga burmeisteri	Omnivore	Ground-Understory	1298	F
Herpetotheres cachinnans	VertFishScav	Ground-Understory-Midhigh	623.58	F
Caracara plancus	VertFishScav	Ground	1078.62	G
Myiopsitta monachus	PlantSeed	Ground-Understory-Canopy	120	G
Amazona aestiva	Omnivore	Understory-Midhigh-Canopy	451	F
Aratinga nenday	PlantSeed	Ground	128	F
Thectocercus acuticaudatus	Omnivore	Ground-Understory-Midhigh-Canopy	171	F
Psittacara leucophthalmus	PlantSeed	Understory-Midhigh-Canopy	158	F
Taraba major	Invertebrate	Ground-Understory-Midhigh	59.2	F
Thamnophilus doliatus	Invertebrate	Ground-Understory-Midhigh	27.03	F
Thamnophilus caerulescens	Invertebrate	Understory-Midhigh	21.1	F
Myrmorchilus strigilatus	Invertebrate	Ground-Understory	23	F
Melanopareia maximiliani	Invertebrate	Ground-Understory	18	F
Rhinocrypta lanceolata	Invertebrate	Ground-Understory	61.9	F
Sittasomus griseicapillus	Invertebrate	Midhigh-Canopy	13.12	F
Xiphocolaptes major	Invertebrate	Ground-Understory-Midhigh	156	F
Campylorhamphus trochilirostris	Invertebrate	Understory-Midhigh	40.8	F
Drymornis bridgesii	Invertebrate	Ground	92.62	F
Lepidocolaptes angustirostris	Invertebrate	Understory-midhig	29.59	F
Furnarius rufus	Invertebrate	Ground-Understory	46.42	G
Furnarius cristatus	Invertebrate	Ground	25.5	F
Phacellodomus sibilatrix	Invertebrate	Ground-Understory-Midhigh	72.2	F
Coryphistera alaudina	Invertebrate	Ground	30	F
Asthenes baeri	Invertebrate	Ground-Understory	17.8	F
Cranioleuca pyrrhophia	Invertebrate	Understory-Midhigh-Canopy	14.9	F
Pseudoseisura lophotes	Invertebrate	Ground	72.2	F

Schoeniophylax phryganophilus	Invertebrate	Ground-Understory	18.6	G
Synallaxis frontalis	Invertebrate	Ground-Understory	14	F
Camptostoma obsoletum	Invertebrate	Midhigh-Canopy	8.1	F
Suiriri suiriri	Invertebrate	Understory-Midhigh	14.53	F
Serpophaga subcristata	Invertebrate	Understory-Midhigh-Canopy	6.6	G
Stigmatura budytoides	Invertebrate	Understory-Midhigh	11.08	F
Sublegatus modestus	Invertebrate	Understory-Midhigh	14	F
Inezia inornata	Invertebrate	Understory-Midhigh-Canopy	12	F
Hemitriccus margaritaceiventer	Invertebrate	Understory-Midhigh	8.4	F
Lathrotriccus euleri	Invertebrate	Understory	11.33	F
Knipolegus striaticeps	Invertebrate	Ground-Understory	11	F
Machetornis rixosa	Invertebrate	Ground	14	G
Pitangus sulphuratus	Omnivore	Ground-Understory-Midhigh	62.85	G
Tyrannus melancholicus	Invertebrate	Midhigh-Canopy	37.4	G
Casiornis rufus	Invertebrate	Understory-Midhigh-Canopy	24.8	F
Myiarchus tyrannulus	Invertebrate	Ground-Understory	35.45	F
Cyclarhis gujanensis	Invertebrate	Understory-Midhigh-Canopy	28.8	F
Vireo olivaceus	Invertebrate	Midhigh-Canopy	16.06	F
Cyanocorax chrysops	Invertebrate	Ground-Midhigh-Canopy	166	F
Troglodytes aedon	Invertebrate	Understory	10.85	G
Polioptila dumicola	Invertebrate	Midhigh-Canopy	7	F
Turdus rufiventris	Omnivore	Ground	69.44	G
Turdus amaurochalinus	FruiNect	Ground-Understory-Midhigh-Canopy	57.9	G
Ammodramus humeralis	PlantSeed	Ground-Understory-Midhigh	15.99	G
Zonotrichia capensis	PlantSeed	Ground	20.31	G
Euphonia chlorotica	FruiNect	Canopy	11	F
Cacicus solitarius	Invertebrate	Understory-Midhigh	79.76	F
Icterus croconotus	FruiNect	Midhigh-Canopy	40.03	F
Icterus pyrrhopterus	Invertebrate	Understory-Midhigh-Canopy	35.44	G
Molothrus bonariensis	Invertebrate	Ground	41.49	G
Setophaga pitiayumi	Invertebrate	Canopy	6.82	F
Sicalis flaveola	PlantSeed	Ground-Understory	16.89	G
Saltatricula multicolor	Omnivore	Understory-Midhigh	22.2	F
Saltator coerulescens	Invertebrate	Understory-Midhigh	54.9	G
Saltator aurantiirostris	Invertebrate	Understory	41.89	G
Microspingus melanoleucus	Omnivore	Ground-Understory	13.1	F

Lophospingus pusillus	Omnivore	Ground-Understory	14.44	F
Paroaria coronata	Invertebrate	Ground-Understory	37.79	G
Paroaria capitata	Invertebrate	Understory-Midhigh	22.3	G

Table S2. Univariate models parameterized at different spatial scales. AICc values are provided in the table below, with numbers in bold showing the lowest AICc.

		Landscape Metric		
Dependent variable	Scale (m)	Forest area	Patch density	Edge density
All birds				
Taxonomic diversity	500	203.788	203.705	203.221
	1000	**203.076**	203.375	203.598
	3000	203.621	**202.334**	**198.213**
Functional diversity	500	-218.092	**-217.394**	-217.314
	1000	-217.288	-217.342	-218.009
	3000	**-220.351**	-217.332	**-219.869**
Phylogenetic diversity	500	70.409	76.716	72.174
	1000	**69.431**	**73.049**	76.215
	3000	75.750	74.321	**67.801**
Forest specialist				
Taxonomic diversity	500	**206.99752**	207.00685	207.18154
	1000	207.34050	207.32252	207.02956
	3000	207.29700	**206.81790**	**205.01640**
Functional diversity	500	-238.1548	-238.9124	**-240.5192**
	1000	-238.2261	**-242.9183**	-240.7892
	3000	**-239.6419**	-238.5254	-238.0717
Phylogenetic diversity	500	**54.9004**	**54.9004**	54.9912
	1000	**49.8879**	55.1091	55.5432
	3000	55.4013	55.6572	**49.8879**
Generalist				
Taxonomic diversity	500	175.01391	175.73738	175.28209
	1000	**175.08994**	174.79787	175.76435
	3000	175.78538	**174.09480**	**174.14330**

For all birds, variables with lower AICc values selected for taxonomic diversity were Forest area (1km) + Patch density (3km) + Edge density (3km), for functional diversity were Forest area (3km) + Patch density (0.5km) + Edge density (3km) and for phylogenetic diversity were Forest area (1km) + Patch density (1km) + Edge density (3km).

For forest birds, variables with lower AICc values selected for taxonomic diversity were Forest area (1km) + Patch density (0.5km) + Edge density (3km), for functional diversity were Forest area (3km) + Patch density (1km) + Edge density (0.5km) and for phylogenetic diversity were Forest area (1km) + Patch density (0.5km) + Edge density (3km).

Capítulo 3

Bird communities in the Dry Chaco of South America: vegetation structure and climate effects

Abstract

Species lead to a complex and dynamic environment affected by external processes. Better understanding the importance of these factors is particularly urgent for the world's tropical dry forest, which is understudied, highly threatened and rapidly disappearing. Building on a unique, field-based bird community dataset, we used multivariate analysis and generalized linear models to test the effects of climate and vegetation structure on bird composition and richness in forest corridors. Our analyses revealed the importance of forest corridors that not only connect the landscape but may facilitate the movement of species, having a high potential for management and connectivity planning. We found significant differences in bird communities to environmental changes when focusing on all birds or when analyzing dry-forest birds only. For all birds, composition revealed preferences of habitat. Birds of open habitats were positively associated with canopy openness, temperature, and relative humidity, while birds to avoid open habitats were positively associated with higher canopy density. The most important variables explaining variations of dry-forest birds were understory and canopy density. Richness increases with temperature for the entire community, yet higher temperatures during the day decrease bird activity. Overall, we showed that bird composition differences were associated with canopy changes, yet richness increased with understory cover. Likewise, our study highlights the importance of maintaining a microenvironment based on local requirements for composition or richness. Moreover, the conservation strategies should be consistent to those requirements to promote the viability of corridors uses that potentially connect the landscape.

Keywords: Gran Chaco, Birds, Microclimate, Paraguay, Land-use, Agricultural impact.

Introduction

Species live in a complex and dynamic environment affected by external processes (Cadotte et al., 2011). Anthropogenic disturbances such as habitat loss and fragmentation change local and regional environmental conditions due to agricultural expansion and intensification (Tilman et al., 2017). Human pressure is particularly intense in the tropics and subtropics, where agriculture continues to expand into remaining natural areas (Lambin and Meyfroidt, 2011; Song et al., 2018), which harbor high and unique biodiversity (Laurance et al., 2014; Roque et al., 2018).

Understanding biodiversity change in the face of agricultural expansion is not trivial because different aspects of habitat change might impact biodiversity differently. Importantly, agricultural expansion change leads to habitat loss and fragmentation (Fahrig, 2003; Foley et al., 2005). There is now considerable empirical evidence, as well as theoretical underpinnings, suggesting that habitat destruction threatens species connected to this habitat through population declines and local extinctions (Haddad et al., 2015; Johnson et al., 2017; Pfeifer et al., 2017). However, when habitat corridors connect forest fragments, its promotes an increase in abundance, favored dispersion and maintained a positive relationship between forest and species (Gonzalez et al., 2010). Despite its importance, the study of corridors demands long-time experiments, also experimental and tracking species and operating at a landscape scale (Machtans et al., 1996). On fragmented landscapes, corridors are often viewed as a management element to increase connectivity, yet the way different species use these connectors still deserves further attention (Beier and Noss, 1998). First, corridors are not always clearly associated with morphological and ecological characteristics because they contribute to maintaining overall landscape connectivity by facilitating the movement of individuals and genes (Gonzalez et al., 2010; Tewksbury et al., 2002). Second, conclusions on ecological corridors have indicated that factors influencing the importance of these landscape elements are highly singular and must be analyzed carefully. However, overall should accomplish the functional and structural connectivity. Finally, it may improve the species' responses to habitat fragmentation and the probability of success in management strategies (Lindenmayer and Nix, 1993).

As habitat loss ensues, landscapes also become more heterogeneous and fragmented, containing a higher diversity of habitats (Fahrig, 2013, 2003). The spatial dynamics may play a key role in species perception (Leibold et al. 2004), and therefore scale effects are species-specific (Hawkins et al., 2003; Rahbek, 2005; Whittaker et al., 2001). It is well known that at large scales, species diversity is related to climate and productivity (Hawkins et al., 2003; Rahbek, 2005). In contrast, at smaller scales dispersal and biological interactions are more important (García and Ortiz-Pulido, 2004; Leibold et al., 2004). Despite scale dynamics, a new complexity level may influence responses, and species diversity is also linked to environmental factors (Ruggiero and Kitzberger, 2004). Climate has been identified not only to have a direct effect on species richness by imposing physiological constraints but to have indirect effects, *e.g.*, changing vegetation structure and productivity (Hawkins et al. 2003). Corridors are exposed to agricultural activities impacts, which may result in changes in habitat quality and climate conditions associated with severe environmental conditions in the forest (Sodhi and Smith 2007), affecting species responses and use of these connectors (Zimbres et al., 2017).

Tropical birds are species with many biological interactions associated with specific habitats, have a high dispersal ability and their taxonomy is well documented (Jetz et al., 2012). Bird responses to environmental changes quickly made them excellent indicators (Foley et al., 2005; Vandewalle et al., 2010). There is considerable empirical evidence, as well as theoretical underpinnings, suggesting an increase in habitat destruction leads to population declines and local extinctions (Haddad et al., 2015; Johnson et al., 2017; Pfeifer et al., 2017). Habitat fragmentation exacerbates this trend, especially for forest species, through the isolation of sub-populations, as well as via edge effects, such as increased nest predation, lower breeding success due to human disturbance, or parasitism (Bierregaard, et al., 1992; Sodhi and Smith, 2007; Wiens, 1999). Importantly, although spatial dynamics and corridors influence bird distribution, and dispersal (Levey et al., 2005), climate conditions also affect the community structure, especially the composition, abundance and richness (Villard et al., 1999; Zelaya et al., 2022). Climatic variations affect the availability of food resources, nesting places, and vegetation structure (Freemark and Merriam, 1986; Meynard and Quinn, 2008). Thus, in regions with high land use change rates, understanding the climate effects on the establishment, composition, and diversity of birds is critical.

Tropical dry forest is considered one of the most threatened regions in the world being agriculture activities the primary cause of tropical dry forest conversion (Miles et al., 2006). Nevertheless, these regions are weakly protected and under-researched, resulting in a gap of conservation planning and action, particularly in South America (Escribano-Avila et al., 2017; Portillo-Quintero and Sánchez-Azofeifa, 2010). There is an urgent need to better understand how biodiversity responds to the increasing human pressure in South America’s dry forests to develop strategies that ensure the conservation of their biodiversity. The Gran Chaco is the largest dry forest ecoregion in South America and has recently been particularly hard-hit by agricultural expansion. Widespread soybean and cattle ranching expansion has turned this region into a global deforestation *hotspot* (Hansen et al., 2013; Kuemmerle et al., 2017).

Within the Chaco extent, deforestation has been rampant in the Paraguayan Chaco since 2010 (Baumann et al., 2022), yet few studies so far from the Paraguayan Chaco understand how landscape change impacts biodiversity. Several laws in Paraguay were designed to protect natural vegetation and forest resources. Yet, one in particular, Law 542/95, requires that 25% of the surface area of farming properties remains forested is predominantly essential. In addition, properties larger than 100 ha are requested by Decree 18,831/86 (Milán and González, 2022), to maintain forested areas at least 100 m wide between agricultural plots, named "windbreaks", which has the principal objective of restraining the north wind pressure and avoid erosions. Although there is no evidence so far that these strips help to protect biodiversity, these do not dismiss its importance as forest elements structurally connect the landscape. Yet such strips should provide an opportunity to maintain landscape connectivity through a functioning network of corridors.

Climate is a key environmental variable in dry environments (Prado and Gibbs, 1993). The complexity of the Dry Chaco microenvironment is related to several interactions and interdependence between temperature increase and humidity, influenced by edge orientation, altitude variations, and matrix type, among other factors (Moreno et al., 2014). While the microhabitat in drylands is very dynamic, is principally correlated with abiotic conditions and determined by canopy cover. The dry forest is composed of a discontinuous canopy cover that distinguish the sunlight as the most predominant variable in the microclimate (Páez and Marco, 2000). Variables such as humidity, solar radiation, and air temperature affect the metabolic rate of animals and plants, producing physiological constraints that limit species distribution, composition, and structure of communities (Hawkins et al. 2003). Thus, local species are expected to have distinctive adaptations for local survival and individual responses to environmental changes (Sekercioglu et al., 2002).

The structure of forest bird communities depends on habitat use and local variables interactions (Walther, 2002). Bird communities are influenced not only by the landscape scale but also by vegetation structure and climatic conditions at the local scale. Such conditions are also important in the Argentinian Chaco (Zelaya et al., 2022), where the reduction of food availability (Lopez de Casenave et al., 1998) compromises the energy balance of species

(Pollock et al., 2015). Richness and species composition of birds are strongly associated to the complexity of vegetation structure, which increases with precipitation in drylands (Gonçalves et al., 2017). Finally, the general patterns of climate and vegetation structure, directly and indirectly, affect bird species (Hawkins et al. 2003) which should be linked to habitat quality and landscape conservation (Gonçalves et al., 2017). Critically, understanding how these factors interact to control resources in habitat selection remains unexplored in the Dry Chaco, yet may contribute not only to evolutionary ecology but also to predicting better responses to climate and habitat change.

We assess the use and importance of forest corridors in the Paraguayan Chaco on maintaining landscape connectivity and attenuating local climate on bird communities. Such linear element has recently undergone the most drastic forest changes in the region. Our main goal is to understand how bird communities use the forest corridors, and how vegetation structure and climate conditions within these forest corridors are in the maintenance of microenvironments capable of supporting bird communities. Specifically, we predicted that bird communities respond negatively to high temperature values, reducing their activity during the day. Also, we asked the following research questions: (1) How do avian diversity (richness and abundance) respond to changes in climate and vegetation structure in forest corridors? (2) What climate and vegetation structure variables influence bird composition the most?

Materials and methods

Study area

The Gran Chaco is a biogeographic region comprising the Wet Chaco and Dry Chaco. The Dry Chaco is the largest tropical dry forest in South America, extending over a flat terrain over an area of 840,000 km² in Argentina, Paraguay, and Bolivia. The Dry Chaco contains a mosaic of xerophytic vegetation formations, including dry forests, scrublands and savannas (Pennington et al. 2000; Werneck 2011). The soils in the Chaco are mainly based on fluvial pedogenesis in the north and derive from eolic sediments and loess material in the south (Navarro et al., 2011). The climate is semiarid with summer maxima of up to 49 °C. There is a strong east-west rainfall gradient (450–700 mm), and marked seasonality, with a dry season in the winter/spring and a rainy season in the summer/autumn. Vegetation can be subjected to low soil moisture and freezing temperatures during the dry season and waterlogging and extremely high temperatures during the rainy season (Pennington et al. 2000).

The Paraguayan Dry Chaco is a region where natural vegetation is dominated by xeromorphic forest and scrubland (Mereles and Rodas, 2014). The vertical structure is depended on soil characteristics, having between on 4-5 layers. The canopy is comprised of 3–4 species and being up to 20-25 meters, as the second layer it has the “matorral” (scrubland) and finally a very scattered understory comprised by thorny and succulent species (Fig. 1).

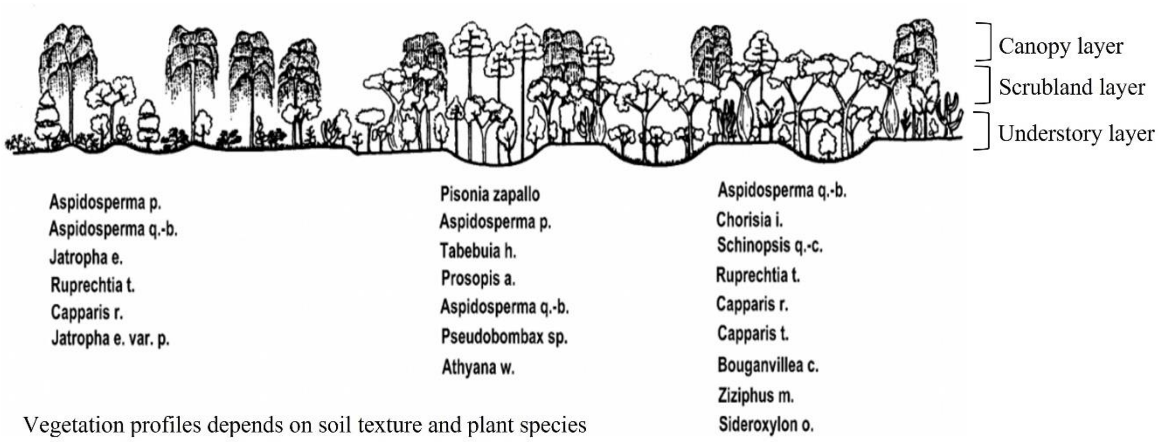


Fig 1. Vegetation profile of xeromorphic forest at the Paraguayan Dry Chaco with the most important vertical layers and the most represent plant species (Adapted from Mereles, 2005).

Most of the natural vegetation is unprotected (16.2% of protected areas; Nori et al. 2016) yet is rapidly converted to agriculture by domestic and international agribusiness actors who establish large farms (Milán and González, 2022), mainly for producing beef for international markets (Baumann et al. 2017; Franco-Solís and Montanía 2021). Despite this general trend, the Paraguayan Chaco contains diverse deforestation dynamics. Deforestation in the central Paraguayan Chaco leads to small and isolated fragments of remaining forests (Mereles and Rodas 2014). In contrast, larger blocks of natural vegetation remain in the landscape in the northern Paraguayan Chaco, where the agricultural frontier currently expands (Vallejos et al., 2015). Notably, private landowners must maintain a narrow strip of forest between agricultural plots, so-called windbreaks (*cortinas*) (hereafter: forest corridors). This aspect gives the singularity to the Paraguayan Chaco landscape.

Bird surveys

We used passive sound recorders to sample bird communities in the Paraguayan Chaco. This non-invasive method helps estimate biodiversity abundance and occurrence while minimizing human disturbance and interferences. Besides, it allows for longer term-monitoring of several vocal species, such as birds (Pérez-Granados and Traba, 2021; Sugai et al., 2019). We surveyed birds at 22 sites (n=22) in forest connectors inside larger cattle ranches (Fig. 2). Sites were selected based on landscape characteristics to include diverse landscape configurations in central and northern Paraguayan Chaco. We installed recorders at 2-meter-height in trees separated at least 1000 meters between sites. We recorded at our sites during two days in September and October of 2019, coinciding with the end of the dry season, a period when most birds in this region initiate breeding. Each recording consisted of 10-minute samples (wave format 48 MHz and 16 bits) during the peak of avian vocal activity (i.e., 05:00 to 08:30 in the morning and 16:00 to 19:00 in the evening) to detect both diurnal and nocturnal birds.

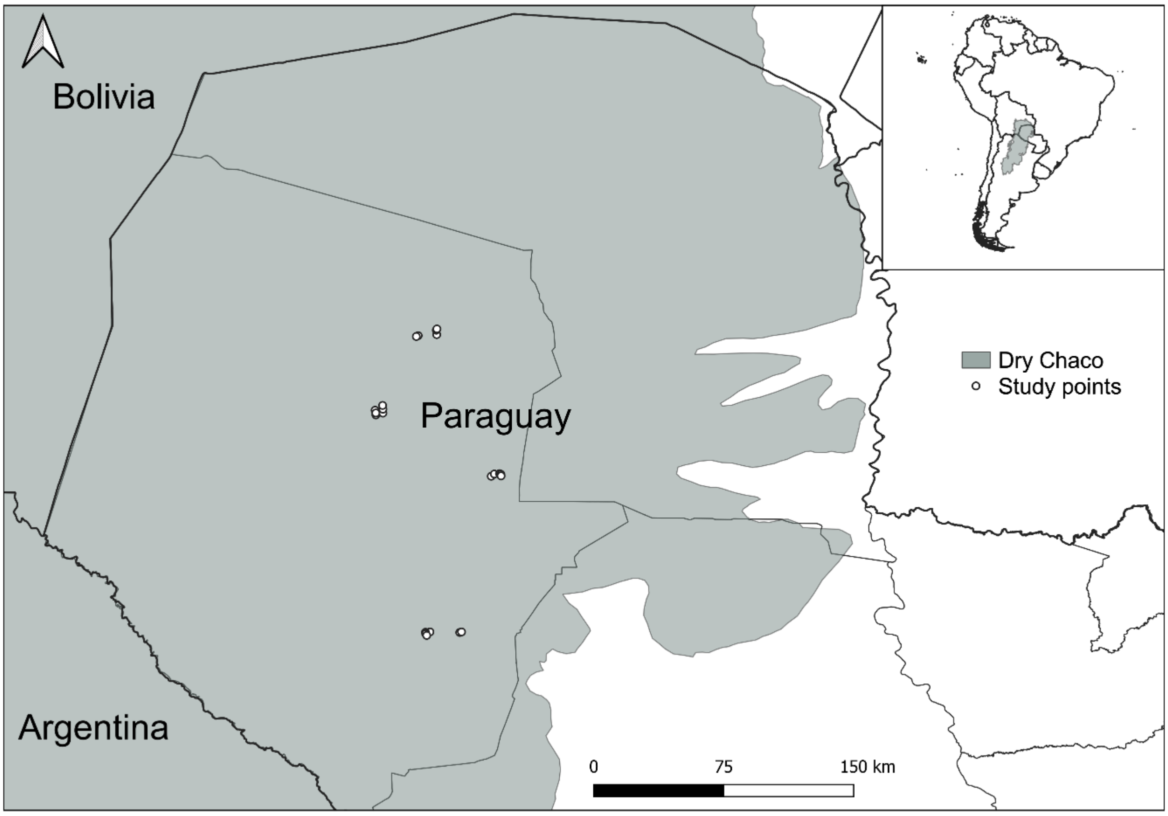


Fig 2. Study area in the Paraguayan Dry Chaco with the 22 sampling forest corridors delimited with a gray line is the Dry Chaco of South America.

We analyzed the recordings manually and automatically. We selected the birds' peak activity time based on field experience, considering the bird activity at the corridors (i.e., 05:20 to 06:30 h for diurnal birds and 18:40 h for nocturnal birds). Bird species were identified manually by the same person (R.C.), listening the recordings (154 independent recordings) helped by a spectrogram produced with Raven Pro 1.6 software (Center for Conservation Bioacoustics, 2019). We only registered persistent singing and excluded songs of flying birds (e.g., songs of flying parrots) and used birds' songs repository for species identification (Xeno-Canto, www.xeno-canto.org; and Macaulay Library www.macaulaylibrary.org), as well as consulting with experts on bird songs from the region. Abundance was calculated by the frequency with which species was detected on the recordings.

Environmental and vegetation predictors

To evaluate the influence of environmental variables on bird communities, we calculated predictor variables representing environmental variables and vegetation structure. We adopted a point-quadrant method in each forest corridor, using the recorder position as the central point. We calculated tree basal area density, understory density, canopy density, and canopy openness to capture the vegetation structure. We calculated tree basal area density based on the nearest four trees (i.e., ≥20 cm of diameter), and for that, we measured the circumference and distance of each tree to the central point. To calculate understory density, we counted the number of segments of a cover pole 200 cm long, with 10-cm segments that were entirely visible from a 10 m distance from the central point. We calculated canopy density and canopy openness based on image values of a fisheye photography taken from a Nikon Coolpix 950 camera. We perform the analyses using the package Hemiphot.R (https://github.com/naturalis/Hemiphot).

We used environmental variables/atmospheric conditions to represent local climate predictors. We collected temperature (TP), relative humidity (RH), and wind speed (WS) from weather data measured during two days by Kestrel 4500 model installed at the central point. We positioned the device vertically looking to the magnetic north for better results. We used the mean value of each variable (two days) to perform the analyses. The sunlight output used was based on 60 readings and displayed a 15 second average, using a photometric sensor LI-250A Light Meter, prior calibration and leveled with a bubble level.

Table 1. Vegetation and environmental variables used to characterize the sampling points at the Paraguayan Dry Chaco.

	Description	Mean [range]
Vegetation structure		
Basal area density (m^2/ha)	Dry forest stand density.	46.88 [8.76 - 162.68]
Understory density	Density of vegetation at the low vertical strata between 0 and 3 m above the ground (Walther, 2002)	0.50 [0.20 - 0.75]
Canopy density	Space within the crown of the highest trees (Walther, 2002). We used a canopy leaf area index, consisting of the light interception to the ground surface area.	1.07 [0.65- 1.69]
Canopy openness	Entrance of light through the canopy. As canopy openness is higher, lighter into the ground.	0.44 [0.34 - 0.66]
Environmental factors		
Sunlight (lux)	Sun light density, intrusion until the understory stratum. One lux (1 lux) of light is a measure of the light density, equivalent to 1 lumen per square meter (lm / m^2).	442.07 [85.5 - 926.7]
Wind speed (km/h)	Air moving from high to low pressure. Wind velocity through the dry forest.	1.45 [0 - 3.75]
Temperature (°C)	Air hotness or coldness registered at the dry forest.	29.07 [16.70 - 34.30]
Relative humidity (%)	Ratio of the vapor pressure of air to its saturation vapor pressure.	46.61 [32.86 – 77.96]

Bird assemblage

We divided our response variables into two groups for the analyses. The first group consisted of all birds (hereafter: all birds), including both forest specialist birds and generalist species that use a variety of habitats, such as forest, forest edges, and open areas. The second group included only dry-forest specialist birds (hereafter: dry-forest birds) that are rarely found in other habitat types. We classified forests based on published habitat associations (Parker III et al. 1996; Dardanelli et al. 2006; Semper-Pascual et al. 2018; Table A1). Finally, we compared the use of corridors by bird communities in an anthropological region and agriculture frontier contexts.

We performed a non-metric multidimensional scaling (NMDS) based on a Bray Curtis similarity index to identify bird assemblage responses. To detect which climate and vegetation variables influence changes in bird composition, we used Multi Response Permutation Procedure (MRPP) (Table S2, Table S3), and to know species contribution to differences among samples (Table S4, Table S5), we used the Indicator Species Analysis (ISA) (Dufrêne and Legendre, 1997). The statistical significance of MRPP and ISA were performed using randomization with 999 random permutations and selected the environmental variables and species indicator based on $p<=0.05$ scores.

Statistical models

We used generalized linear models (GLM) to understand the diversity patterns. First, we checked for outliers, normal distribution, and the relationships between response and predictor variables using scatterplots. Second, we performed a canonical correspondence analysis (CCA) to select uncorrelated variables: basal area density, understory density, canopy density for vegetation structure, temperature, and wind speed for climate factors (Fig A1). We tested all the selected variables for all birds and dry-forest birds, including climate and vegetation.

Next, we performed a model selection to test all combinations of best-performing predictor variables using the R package “MuMIn” (Barton 2022) . We selected the best-performing model based on the AICc, considering models with ΔAICc <2 (Table S6) as having equally strong empirical support and plausibility (Burnham et al., 2011; Burnham and Anderson, 2002) and then averaged these best-performing models using the R package to derive conditional average coefficients.

Automatic analysis

We performed automatic analyses to calculate acoustic indices to identify the effects of temperature. Acoustic indices convert bird signatures to assess the spatial and temporal distributions of different birds in ecosystems (Pijanowski et al., 2011). This method is helpful for quick assessments, reduces the time of processing records, and can be associated with species diversity or species activity, providing a rapidly assessed biodiversity (Machado et al., 2017; Pijanowski et al., 2011; Sueur et al., 2014)

We selected two indices: Acoustic Diversity Index (ADI) and Bioacoustics Index (BI), as both shows significant association with avian species richness (Fuller et al., 2015). ADI is calculated based on Shannon entropy, and BI was designed to capture all sound across the frequencies range (Boelman et al., 2007). To calculate ADI and BI, we first divided our dataset into four hours in the morning (05:00-05:59, 06:00-06:59, 07:00-07:59, 08:00-08:59). Then, we selected four recordings per hour (each 10 min duration) to split each into one-minute duration samples, which resulted in 1,170 files. Finally, we used the standard parameters of the R packages "soundecology" (Villanueva-Rivera et al., 2011) and the R packages "seewave" (Sueur et al., 2008) to analyze the files. The ADI, BI and temperature corresponded to an hour average for each site. Hourly analyses were repeated samples, by hour of day within sites, and represents not independent data points. We used a mixed model using the R package "lmer" (Bates et al., 2015), being 'time' the random structure. All the analyses were performed in R statistical software (R Core Team, 2021).

Results

We identified 80 terrestrial bird species, of which 21 birds were dry-forest birds (16.2% of all species recorded). Three species (2.4%) were ubiquitous, occurring in all sites, of which all were generalist birds. The most abundant birds recorded in all sites were *Lepidocolaptes angustirostris* (78 records, 5.52%), *Suiriri suiriri* (76 records, 5.38%), *Furnarius rufus* (70 records, 4.96%).

Bird assemblage composition

Bird composition did not diverge between regions with a different agricultural land cover but between the same agricultural landscape (Table S1, Fig A2), this indicated that some forest corridors from both regions shared a similar set of birds, and bird compositions differ within the same region.

For all birds, the vegetation predictors that influenced communities the most were canopy density and openness, while climate predictors were temperature, wind speed, and relative humidity. For dry-forest birds, the most important predictors were canopy density and wind speed. Importantly, for all birds, the results confidence was on the limit of acceptance value (stress= 0.2020), while for dry-forest birds it was acceptable (stress = 0.1966).

For all birds (Fig 3), *Furnarius cristatus, Cranioleuca pyrrophia, Rhinocrypta lanceolata* and *Stigmatura budytoides* were positive associated with canopy openness; *Megacops choliba* and *Casiornis rufus* were positive associated with canopy density; *Knipolegus striaceps, Aratinga nenday, Inezia inornata* and *Paroaria coronata* were positive related to temperature, contrary to large body size birds: *Nothura maculosa, Chunga burmeisteri* and *Nystalus maculatus* that were positively associated with relative humidity. *Leptotila verreauxi* was positively associated with wind speed. For dry-forest birds (Fig 3), *Knipolegus striaceps, Lophospingus pusillus* positively related to canopy density and negative associated with *Nothoprocta cinerascens* and *Ortalis canicollis,* contrary to *Microspingus melanoleucus, Myrmorchilus strigilatus, and Aratinga nenday* negative associated with wind speed.

Large body size birds that included *Nothura maculosa, Chunga burmeisteri, Nothoprocta cinerascens* and *Ortalis canicollis* were abundant at the corridors, most of them associated with variables of open habitats.

Diversity patterns

Generalized linear models showed influences of climate and vegetation structure on birds' communities. For all birds, climate conditions had significant influences, being the temperature the most important (Table 2) with a positive relation (Fig 4). For dry-forest birds, vegetation structure had significant influences, being understory density and canopy density the most important (Table 2). The richness of dry-forest birds increases with understory density (Fig 4).

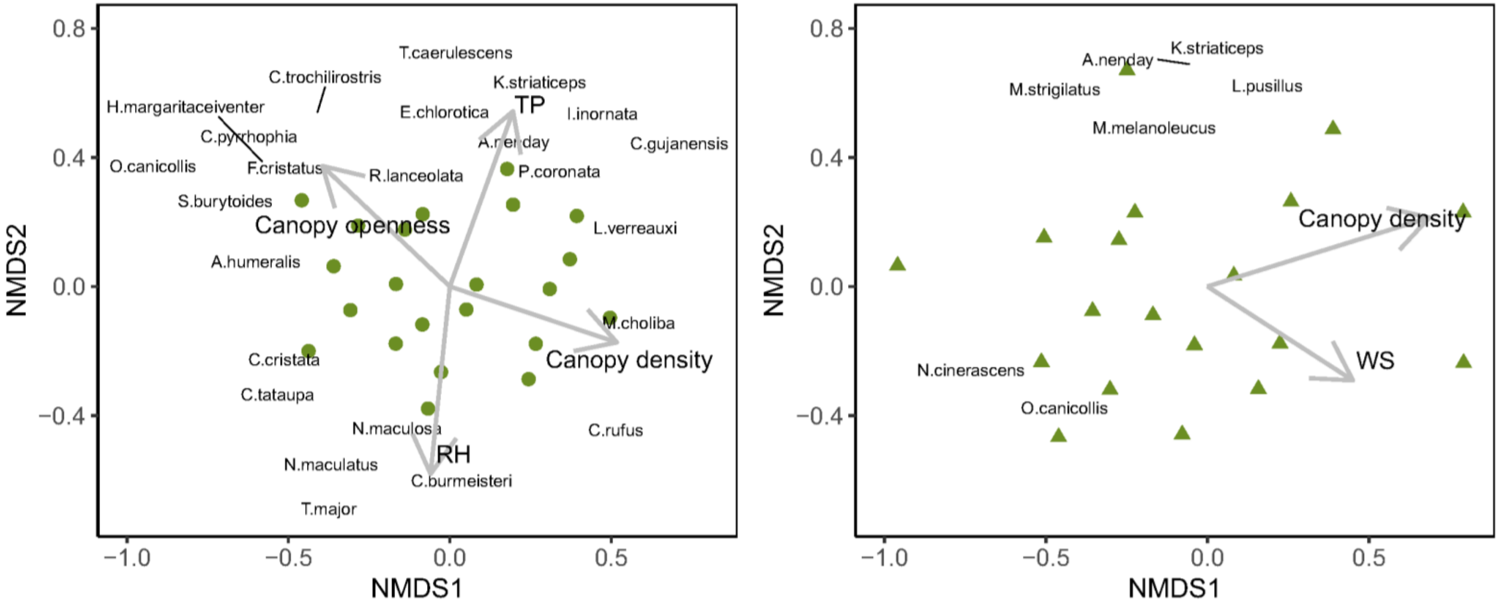


Fig 2. The Non-Metric Multidimensional Scaling (NMDS) ordination plot of birds in corridors of the Paraguayan Chaco on the basis of Bray-Curtis's dissimilarity. Environmental variables and species of birds that significantly affected the composition between birds' communities. Ordination was performed considering both all bird species (circles) and dry-forest birds (triangles).

Table 2. Average-model output from GLM models examining vegetation structure and climate factors correlates of dry-forest specialist and overall bird species richness.

Response variable	Predictor variable	Relative importance	Estimate	SD
Dry-forest specialist	Intercept		1.9104	0.4802
	Understory density	0.62	0.9254	0.4990
	Canopy density	0.39	-0.3940	0.3105
All birds	Intercept		3.1509	0.2456
	Temperature	0.65	0.0129	0.0068

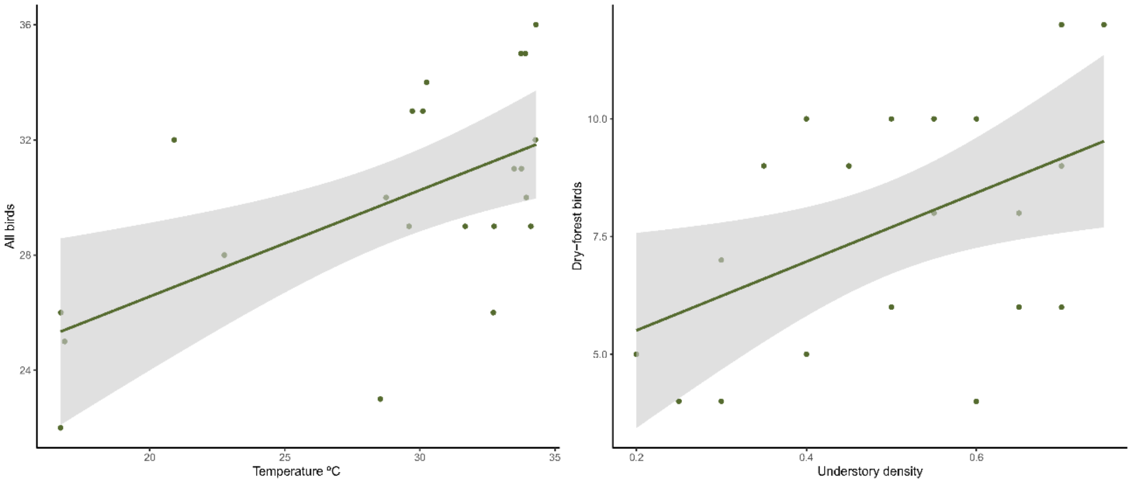


Fig 4. Climate and vegetation predictors relate to richness of all birds (left) and dry forest birds (right). GLM significant results ($P < 0.05$) and gray bands show 95% confidence bands.

Temperature effects

We identified temperature going higher during the morning while decreasing bird activity (Fig 5). Bird activities responded negatively to temperature increases during the morning for both indices (Table S7), ADI was β= -0.00535, SD= 0.00278 and BI was β= -0.02365, SD= 0.03726.

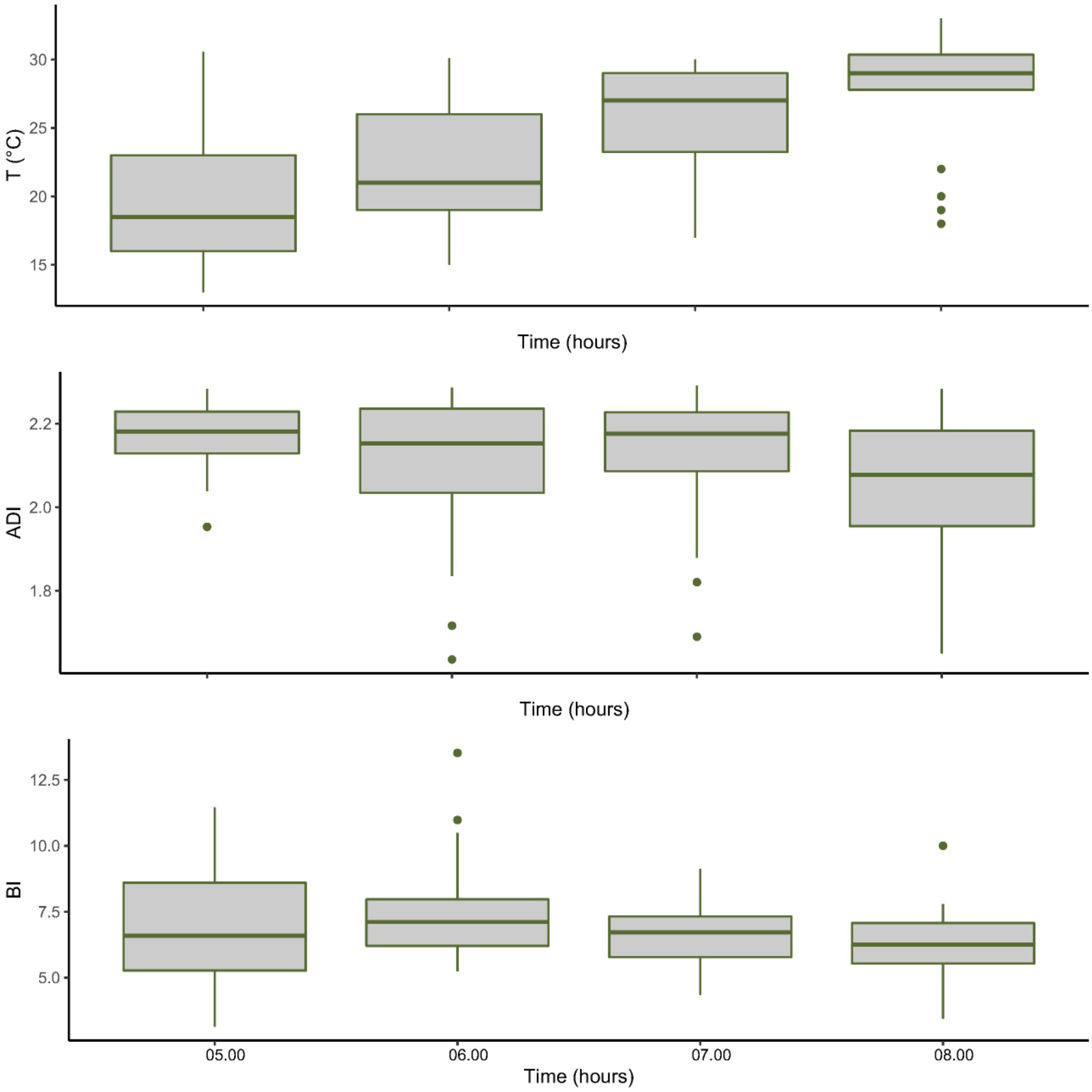


Fig 5. Temperature and bird activity represented by two acoustic indexes: Acoustic diversity index (ADI) and Bioacoustics Index (BI) responses during four hours in the morning at the corridors of the Paraguayan Dry Chaco. Box plots show median, quartiles, as well as maximum and minimum values.

Discussion

Land use change due to agricultural expansion is a key driver of biodiversity loss, especially in the forest tropics. However, understanding how environmental consequences of habitat changes, particularly vegetation structure and climate factors and their relation to biodiversity remains unknown. Currently, the tropical dry forest is affected by being understudied, yet disappearing faster in South America. We provide, to our knowledge, the first assessment of the effects of climate and vegetation structure on avian communities in the Dry Chaco, a global deforestation hotspot. Our study contributes with four main insights. First, bird’s species were using the forest corridors, which not only connect the landscape but may facilitate the movement of species, having a high potential for management and connectivity planning. Second, our study revealed significant differences in the responses of bird communities to environmental changes when focusing on all birds or when analyzing dry-forest birds only. For all birds, composition revealed preferences of habitat. Birds of open habitats were positively associated with canopy openness, temperature, and relative humidity, while birds that avoid open habitats were positively associated with higher canopy density. This highlight the importance of the forest to maintain a microhabitat for birds that avoid open habitats, being more sensible to changes in vegetation and climate effects. Third, richness increases with temperature for all birds. Contrary, the most important variables explaining variations of dry-forest birds were understory density. This emphasized different responses when focus on all birds to more specialist birds, and also the importance of vegetation structure in the dry forest, even lower strata, especially for the dry season. Four, even though increase in temperature may contribute with richness of all birds, higher temperatures during the day decrease bird activity. This is especially important for the dry forest, where temperature raising during the day affects bird activities, with many conservation concerns to maintain an effective microclimate.

Our first main finding highlights forest corridors importance to connect the landscape, facilitating the movement of species, having a high potential for management and connectivity planning. Our analyses confirm those connectors currently are habitat of bird communities during the day and night, highlighting their potential as dispersal corridors for bird communities. The forest remnants connect the landscape of our study area within cattle pastures in private landholdings. However, since the absence of conservation objectives, those corridors are permanently exposed to external pressures due to agricultural activities, which makes it challenging to maintain the vegetation structure and quality. Besides spatial connectivity, other factors would determine its effectiveness as functional connectivity, like spatial configuration and vegetation structure. Although, the corridors may contribute to structural attributes that promote connectivity, dispersal abilities of species should influenced the habitat use (Díaz Vélez et al., 2015). Corridors may improve movements between patches, but this does not necessarily ensure functional connectivity. We found that even near corridors from the same region support different communities of birds. Corridors differ structurally, and even agricultural land cover may drive changes. The intrinsic variables related to habitat quality and landscape structure may exert predominant effects on birds. Considerable dissimilarities between corridors structure, especially related to different quality, shape, and length, may guarantee functional connectivity (Pérez-Hernández et al., 2015).

Our second main finding revealed significant differences in the responses of bird communities to environmental changes when focusing on all birds or when analyzing dry-forest birds only. For all birds, composition revealed preferences of habitat. Birds of open habitats were positively associated with canopy openness, temperature, and relative humidity, while birds that avoid open habitats were positively associated with higher canopy density. This highlight the importance of the forest to maintain a microhabitat for birds that avoid open habitats, being more sensible to changes in vegetation and climate effects. Previous studies have suggested that vegetation cover and microclimatic affect species richness and composition of bird species (Gonçalves et al., 2017; Loaiza et al., 2020; Meynard and Quinn, 2008). For both communities, canopy structure was the most important variable influencing bird composition. The Dry Chaco has homogenous vegetation, dominated by xerophytic trees and deciduous leaf vegetation with an integrated closed shrub stratum and a less abundant herbaceous understory (Marchesini et al., 2020). The synergistic effects of vegetation structure and climate mediate the regulation of the Dry Chaco microenvironment, while forest canopy establishes the microhabitat impacting the stratum composition, its discontinuous canopy cover make the sunlight the most predominant variable in the microclimate (Páez and Marco, 2000). Therefore, the area covered by vegetation would determine the amount of light intercepted or absorbed, as well as the rainfall hitting the ground, changing the vertical stratum (Marchesini et al., 2020). Moreover, canopy complexity should facilitate or constrain the dispersion of birds and establish a foraging diversity. For all birds group, bird composition revealed habitat preferences, suggesting the existence of different bird assemblages. Climatic variables influencing directly on birds reveal important physiological constraints, such as thermoregulation and water stress (Hawkins et al., 2003), especially in dry forests, where temperatures are extreme (Castaño-Villa et al., 2014; Pollock et al., 2015). Birds of open habitats tolerate higher climate stresses than forest specialist birds, which may experience limited responses to disturbances in vegetation structure and climate conditions (Tabarelli et al., 2012). Although some dry-forest birds, such as *Furnarius cristatus, Cranioleuca pyrrophia, Rhinocrypta lanceolata*, and *Stigmatura budytoides*, as well as large body size birds like *Nothura maculosa*, *Chunga burmeisteri, Nothoprocta cinerascens* and *Ortalis canicollis* were associated with open habitats, they might have high dependence to the dry forest resources (Dardanelli et al., 2006). The habitat structure affects the composition of birds, which may explain the coexisting of species (Castaño-Villa et al., 2014), including large-bodied bird species more common in thinned or open habitats (Remsen and Robinson, 1990). Large body size birds registered in our study occupied a specific niche and may exclude several species from the denser vegetation (Pearson, 1971).

Our third main finding correlate richness of all birds to increases in temperature. Contrary, the most important variables explaining variations of dry-forest birds were understory density. This emphasized different responses when focus on all birds to more specialist birds, and the importance of vegetation structure in the dry forest, even lower strata, especially for the dry season. Birds' responses corresponded to the beginning of the day. Thus, the temperature may increase bird activities. Other studies found similar responses, being temperature the most important environmental factor driving birds' responses in a dry forest (Loaiza et al., 2020; Zelaya et al., 2022). Yet also indicate that temperature is regulated by structural growth of forest vegetation (Zelaya et al., 2022) and the type of vegetation (i.e., forest or scrubland) (Loaiza et al., 2020). The richness of dry-forest birds increases with understory density in the Chaco. Canopy density decrease during the dry season and only older forest maintain a closed canopy cover (Kalacska et al., 2005). Birds of the understory stratum are less impacted by direct sunlight than canopy birds (Walther, 2002). Therefore, this stratum may contribute the most to foliage density in the dry forest (Pearson, 1971) specially during the dry season. Importantly, dry-forest birds are best adapted to dry forest conditions yet susceptible to habitat transformation (Tabarelli et al., 2012). Indeed, to avoid contrasting habitats, birds of the Dry Chaco adapted their activities during the day. It means a vertical shift in the stratum distribution, beginning from the upper strata to the lower strata during the day (Pearson, 1971) or even move to mature forest with more stable microclimate .

Our four main finding highlight the key role of temperature on bird communities, even though may contribute with richness, higher temperatures during the day decrease bird activity. This is especially important considering the dry forest where temperature raising during the day with up to 47°C in summer months, affecting bird activities, with many conservation concerns to maintain an effective microclimate. The richness of all birds increased with temperature, yet higher temperatures during the day decreased birds' activities. Hence, temperature rise during the day may have adverse effects. The Dry

Chaco has a semiarid climate with a dry period during the cool winter months. Importantly, the dry period is characterized by a substnatial reduction in the intensity and duration of the hydrological regimes, traduces in a reduction of vegetation activity (Marchesini et al., 2020). This conditions constraints bird activities, reduced survival in the heat and desiccation (Woodworth et al., 2018). Additionally, this region is predicted to experience significant climate changes in the future (Siyum, 2020). The predictions highlighted frequent dry events and the global average temperature increase by 2050, promoting environmental changes that lead to species responses at all scales (Walther et al., 2002). Under these circumstances, vegetation cover plays a key role in water balance during the dry season in semiarid regions (Marchesini et al., 2020; Rodriguez et al., 2020). On the contrary, the predominantly pressure of agricultural expansion continues to threaten the dry forest and, therefore, the regional water balance, including the functioning of this ecosystem in the long term (Gasparri and Baldi, 2013; Rodriguez et al., 2020).

Our study relied on a unique, field-based bird community dataset using acoustic recorders in the Dry Chaco. Still, we count on some limitations to be mentioned. First, our study period corresponded to the dry season. It is well known that vegetation structure fluctuates in the dry and rainy seasons, gradually increasing or decreasing its complexity. During dry season, for example, the deciduous trees lose their leaves (Loaiza et al., 2020). This affects birds' behavior and richness (Gonçalves et al., 2017) and may influence both expansions or shrinking of their vertical foraging and resource availability (Pearson, 1971). Second, we are accounting for a local scale assessment, but as we look for the importance of corridor in the landscape, it is a regional scale. This includes the structure of the landscape (e.g., wider corridors and edge effects), which is known to influence birds of the Chaco (Lopez de Casenave et al. 1998; Mastrangelo and Gavin 2014). Third, we do not include habitat disturbances (i.e. selective logging, cattle intrusion) that affects forest cover (Gasparri and Baldi, 2013) and therefore, surely influences bird responses (Ribeiro et al., 2021). Finally, interspecific interactions at a local scale (Pearson, 1971), including biotic interactions and competition, may act as a key driver for changing communities at local scales.

Two local vegetation elements mainly explain birds' composition and richness: tree cover, with dense canopy harboring birds that avoid open habitats, and understory cover, critical in forests of the low canopy (Meynard and Quinn, 2008). On the other hand, bird communities seem to be highly influenced by climate conditions. Both factors are closely related to the corridor's habitat quality and conservation status (Gonçalves et al., 2017). The climate during the dry season, intensified by forest degradation, reshapes the microenvironment and exacerbates the dry forest's climate constraints, creating abiotic conditions that may physiologically challenge bird activities (Pollock et al., 2015). Previous studies suggested that forest degradation decreases the forest cover, and climate constraints during the dry season altered the forest stratum, negatively impacting the understory vegetation due to water scarcity and frost (Gasparri and Baldi, 2013; Marchesini et al., 2020). The most common forest disturbances in the Dry Chaco include selective logging, cattle intrusion, firewood and anthropic fires (Gasparri and Baldi, 2013; Ribeiro et al., 2021). Notably, the low canopy extent and a shrub layer of the Dry Chaco (i.e., canopy cover extent of 15 meters) (Páez and Marco, 2000) are highly vulnerable to degradation impacts. Selective logging and cattle intrusion reduced the forest's habitat quality, afecting canopy and understory cover. Thus, creating a heterogeneity on the vertical cover with negative effects on mammals and bird communities, especially for forest birds' dependent species (Ribeiro et al., 2021; Zimbres et al., 2017).

Both temporal and spatial variation patterns drive biodiversity patterns. Habitat loss and fragmentation in the Chaco are considered significant threats, driving spatial changes in the landscape (Kuemmerle et al., 2017). Although there is a lack of studies investigating connectivity in the Chaco, it is one of the most conservation strategies suggested (Mereles et al., 2019). Only a few studies have shown bird communities' responses to landscape connectivity in the Dry Chaco, finding that corridors analyzed as islands were primarily composed of generalist birds. Otherwise, while connectivity increase, the richness of endemic and forest specialist birds also increases (Areskoug 2001). Birds movements were promoted by functional connectivity in the Chaco, favored by the presence of small fragments to slit distances between larger fragments but also reducing the distance between forest patches (Díaz Vélez et al., 2015). We found that birds using canopy and understory cover explained better variation in richness and composition of species. Birds from the canopy are capable of moving across open areas. Nevertheless, many understory species are highly dispersal limited, becoming critical in colonization (Pearson, 1971) unless the patch is contiguous with existing mature forest (Bradfer-Lawrence et al., 2018). Thus, the dispersal abilities of understory species are likely to be more affected than canopy species. Consequently, compositions of the understory stratum may be highly variable within guild structures, an excellent indicator of the disturbance levels (Bradfer-Lawrence et al., 2018; Loaiza et al., 2020).

The Dry Chaco is receiving huge human pressure from the exceptionally high rates of land use changes and climate, which only can be confronted by creating and implementing appropriate public policies and conservation management actions. Otherwise, it will not be possible to ensure the desirable sustainable development and the correct use of natural renewable resources (Siyum, 2020). Corridors are a structural element increasing the connectivity of forest fragments in the landscape of the Dry Chaco. Besides its importance in avoiding erosion in fragmented landscapes, corridors can also provide suitable habitats for bird species. Therefore, it is necessary to call attention to and prioritize corridors under land use and climate change scenarios. We suggest adopting best practices and well-planned actions to properly conserve the integrity of these connectors, which guarantees their incursion as protected areas or management areas to avoid vegetation degradation. To this end, it would promote increasing the basal area, enriching the canopy, and understory with scrubland species, to ensure its biological and ecological importance. Consequently, it is the potential for functional connectivity.

Acknowledgements

We are grateful to the Brazilian Ministry of Education (CAPES) for RC's PhD scholarship. We thank the German Academic Exchange (DAAD-CAPES) and Humboldt-Universität zu Berlin for hosting RC during a research stay. We also thank Rufford Small Grants Foundation (#28259-1) and the Graduate Program in Ecology, University of Brasilia (CAPES/PROEX) for help in the purchase of recordings and the financial support for the fieldwork in the Chaco, Paraguay. We are indebted to Hugo del Castillo and Lucas Cañete for assistance in the fieldwork, and all landowners for granting access to their properties.

Data availability statement

Data are available from the authors with the permission of the Biodiversity Conservation Planning Laboratory – LaBIO, Department of Zoology – Institute of Biological Sciences - University of Brasilia.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Funding

This work was supported by the Rufford Small Grants Foundation under Grant number 28259-1; and CAPES/PROEX under Grant number 0769/2020.

References

Barton, K., 2022. MuMIn: Multi-Model Inference [WWW Document]. R Packag. Version 1.46.0. URL https://cran.r-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. lme4: Linear mixed-effects models using Eigen and S4.

Baumann, M., Gasparri, I., Piquer-Rodríguez, M., Gavier Pizarro, G., Griffiths, P., Hostert, P., Kuemmerle, T., 2017. Carbon emissions from agricultural expansion and intensification in the Chaco. Glob. Chang. Biol. 23, 1902–1916. https://doi.org/10.1111/gcb.13521

Baumann, M., Gasparri, N.I., Buchadas, A., Oeser, J., Meyfroidt, P., Levers, C., Romero-Muñoz, A., le Polain de Waroux, Y., Müller, D., Kuemmerle, T., 2022. Frontier metrics for a process-based understanding of deforestation dynamics. Environ. Res. Lett. https://doi.org/10.1088/1748-9326/ac8b9a

Beier, P., Noss, R.F., 1998. Do habitat corridors provide connectivity? Conserv. Biol. 12, 1241–1252. https://doi.org/10.1111/j.1523-1739.1998.98036.x

Bierregaard, R.O., Lovejoy, T.E., Kapos, V., Hutchings, R.W., 1992. The Biological Dynamics of Tropical Rainforest Fragments. Bioscience 42, 859–866. https://doi.org/10.2307/1312085

Boelman, N.T., Asner, G.P., Hart, P.J., Martin, R.E., 2007. Multi-Trophic invasion resistance in Hawaii: bioacoustics, field surveys, and airborne remote sensing. Ecol. Appl. 17, 2137–2144. https://doi.org/10.1890/07-0004.1

Bradfer-Lawrence, T., Gardner, N., Dent, D.H., 2018. Canopy bird assemblages are less influenced by habitat age and isolation than understory bird assemblages in Neotropical secondary forest. Ecol. Evol. 8, 5586–5597. https://doi.org/10.1002/ece3.4086

Burnham, K.P., Anderson, D.R., 2002. Multimodel inference: A Practical Information-Theoretic Approach, Sociological Methods and Research.

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65, 23–35. https://doi.org/10.1007/s00265-010-1029-6

Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: Functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48, 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Castaño-Villa, G.J., Ramos-Valencia, S.A., Fontúrbel, F.E., 2014. Fine-scale habitat structure complexity determines insectivorous bird diversity in a tropical forest. Acta Oecologica 61, 19–23. https://doi.org/10.1016/j.actao.2014.10.002

Center for Conservation Bioacoustics, 2019. Raven Pro: Interactive Sound Analysis Software [Computer software].

Dardanelli, S., Nores, M.L., Nores, M., 2006. Minimum area requirements of breeding birds in fragmented woodland of Central Argentina. Divers. Distrib. 12, 687–693. https://doi.org/10.1111/j.1472-4642.2006.00266.x

Díaz Vélez, M.C., Silva, W.R., Pizo, M. a, Galetto, L., 2015. Movement Patterns of Frugivorous Birds Promote Functional Connectivity among Chaco Serrano Woodland Fragments in Argentina. Biotropica 47, 475–483. https://doi.org/10.1111/btp.12233

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366. https://doi.org/10.2307/2963459

Escribano-Avila, G., Cervera, L., Ordóñez-Delgado, L., Jara-Guerrero, A., Amador, L., Paladines, B., Briceño, J., Parés-Jiménez, V., Lizcano, D.J., Duncan, D.H., Iván Espinosa, C., 2017. Biodiversity patterns and ecological processes in Neotropical dry forest: the need to connect research and management for long-term conservation. Neotrop. Biodivers. 3, 107–116. https://doi.org/10.1080/23766808.2017.1298495

Fahrig, L., 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. J. Biogeogr. 40, 1649–1663. https://doi.org/10.1111/jbi.12130

Fahrig, L., 2003. Effects of Habitat Fragmentation on Biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science (80-.). https://doi.org/10.1126/science.1111772

Franco-Solís, A., Montanía, C. V., 2021. Dynamics of deforestation worldwide: A structural decomposition analysis of agricultural land use in South America. Land use policy 109, 105619. https://doi.org/10.1016/j.landusepol.2021.105619

Freemark, K.E., Merriam, H.G., 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biol. Conserv. 36, 115–141. https://doi.org/10.1016/0006-3207(86)90002-9

Fuller, S., Axel, A.C., Tucker, D., Gage, S.H., 2015. Connecting soundscape to landscape: Which acoustic index best describes landscape configuration? Ecol. Indic. 58, 207–215. https://doi.org/10.1016/j.ecolind.2015.05.057

García, D., Ortiz-Pulido, R., 2004. Patterns of resource tracking by avian frugivores at multiple spatial scales: Two case studies on discordance among scales. Ecography (Cop.). 27, 187–196. https://doi.org/10.1111/j.0906-7590.2004.03751.x

Gasparri, N.I., Baldi, G., 2013. Regional patterns and controls of biomass in semiarid woodlands: Lessons from the Northern Argentina Dry Chaco. Reg. Environ. Chang. 13, 1131–1144. https://doi.org/10.1007/s10113-013-0422-x

Gonçalves, G.S.R., Cerqueira, P.V., Brasil, L.S., Santos, M.P.D., 2017. The role of climate and environmental variables in structuring bird assemblages in the Seasonally Dry Tropical Forests (SDTFs). PLoS One 12, 1–16. https://doi.org/10.1371/journal.pone.0176066

Gonzalez, P., Neilson, R.P., Lenihan, J.M., Drapek, R.J., 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. Glob. Ecol. Biogeogr. 19, 755–768. https://doi.org/10.1111/j.1466-8238.2010.00558.x

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1, 1–9. https://doi.org/10.1126/sciadv.1500052

Hansen, M.C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S. a, Tyukavina, a, Thau, D., Stehman, S. V, Goetz, S.J., Loveland, T.R., Kommareddy, a, Egorov, a, Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of

21st-century forest cover change. Science 342, 850–3. https://doi.org/10.1126/science.1244693

Hawkins, B.A., Field, R., Cornell, H. V., Currie, D.J., Guégan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E., Turner, J.R.G., 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology. https://doi.org/10.1890/03-8006

Jetz, W., McPherson, J.M., Guralnick, R.P., 2012. Integrating biodiversity distribution knowledge: Toward a global map of life. Trends Ecol. Evol. 27, 151–159. https://doi.org/10.1016/j.tree.2011.09.007

Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L., Wilmshurst, J.M., 2017. Biodiversity losses and conservation responses in the Anthropocene. Science (80-.). 356, 270–275. https://doi.org/10.1126/science.aam9317

Kalacska, M.E.R., Sánchez-Azofeifa, G.A., Calvo-Alvarado, J.C., Rivard, B., Quesada, M., 2005. Effects of season and successional stage on leaf area index and spectral vegetation indices in three mesoamerican tropical dry forests. Biotropica 37, 486–496. https://doi.org/10.1111/j.1744-7429.2005.00067.x

Kuemmerle, T., Altrichter, M., Baldi, G., Cabido, M., Camino, M., Cuellar, E., Cuellar, R.L., Decarre, J., Díaz, S., Gasparri, I., Gavier-Pizarro, G., Ginzburg, R., Giordano, A.J., Grau, H.R., Jobbágy, E., Leynaud, G., Macchi, L., Mastrangelo, M., Matteucci, S.D., Noss, A., Paruelo, J., Piquer-Rodríguez, M., Romero-Muñoz, A., Semper-Pascual, A., Thompson, J., Torrella, S., Torres, R., Volante, J.N., Yanosky, A., Zak, M., 2017. Forest conservation: Remember Gran Chaco. Science (80-.). 355, 465 LP – 465. https://doi.org/10.1126/science.aal3020

Lambin, E.F., Meyfroidt, P., 2011. Global land use change, economic globalization, and the looming land scarcity. Proc. Natl. Acad. Sci. U. S. A. 108, 3465–3472. https://doi.org/10.1073/pnas.1100480108

Laurance, W.F., Sayer, J., Cassman, K.G., 2014. Agricultural expansion and its impacts on tropical nature. Trends Ecol. Evol. 29, 107–116. https://doi.org/10.1016/j.tree.2013.12.001

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: A framework for multi-scale community ecology. Ecol. Lett. 7, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Levey, D.J., Bolker, B.M., Tewksbury, J.J., Sargent, S., Haddad, N.M., 2005. Ecology: Effects of landscape corridors on seed dispersal by birds. Science (80-.). 309, 146–148. https://doi.org/10.1126/science.1111479

Lindenmayer, D.B., Nix, H.A., 1993. Ecological Principles for the Design of Wildlife Corridors. Conserv. Biol. 7, 627–631. https://doi.org/10.1046/j.1523-1739.1993.07030627.x

Loaiza, C., Montenegro, O.L., King, D., Spínola, M., Palacio, L.A., Rudas, A., 2020. Variation in abundance and habitat relationship of three understory insectivorous birds in a disturbed landscape of Neotropical dry forest of Colombia. Avian Res. 11, 1–12. https://doi.org/10.1186/s40657-020-00219-4

Lopez de Casenave, J., Pelotto, J.P., Caziani, S.M., Mermoz, M., 1998. Responses of avian assemblages to a natural edge in a Chaco semiarid forest in Argentina. Auk 115, 425–435.

Lopez De Casenave, J., Pelotto, J.P., Caziani, S.M., Mermoz, M., Protomastro, J., 1998. Responses of avian assemblages to a natural edge in a chaco semiarid forest in Argentina. Auk 115, 425–435. https://doi.org/10.2307/4089201

Machado, R.B., Aguiar, L., Jones, G., 2017. Do acoustic indices reflect the characteristics of bird communities in the savannas of Central Brazil? Landsc. Urban Plan. 162, 36–43. https://doi.org/10.1016/j.landurbplan.2017.01.014

Machtans, C.S., Villard, M.-A., Hannon, S.J., 1996. Use of Riparian Buffer Strips as Movement Corridors by Forest Birds. Conserv. Biol. 10, 1366–1379. https://doi.org/10.1046/j.1523-1739.1996.10051366.x

Marchesini, V.A., Nosetto, M.D., Houspanossian, J., Jobbágy, E.G., 2020. Contrasting hydrological seasonality with latitude in the South American Chaco: The roles of climate and vegetation activity. J. Hydrol. 587, 124933. https://doi.org/10.1016/j.jhydrol.2020.124933

Mastrangelo, M.E., Gavin, M.C., 2014. Impacts of agricultural intensification on avian richness at multiple scales in Dry Chaco forests. Biol. Conserv. 179, 63–71. https://doi.org/10.1016/j.biocon.2014.08.020

Mereles, M.F., 2005. Una aproximación al conocimiento de las formaciones vegetales del chaco boreal, Paraguay. Rojasiana 6, 5–48.

Mereles, M.F., Céspedes, G., Cartes, J.L., Goerzen, R., Egea-Elsam, J. De, Rodríguez, L., Yanosky, A., Villalba, L., Weiler, A., Cacciali, P., 2019. Biological Corridors as a Connectivity Tool in the Region of the Great American Chaco: Identification of Biodiversity Hotspots in the Ecoregions of the Paraguayan Chaco. Res. Ecol. 2, 27–36. https://doi.org/10.30564/re.v2i1.1324

Mereles, M.F., Rodas, O., 2014. Assessment of rates of deforestation classes in the Paraguayan Chaco (Great South American Chaco) with comments on the vulnerability of forests fragments to climate change. Clim. Change 127, 55–71. https://doi.org/10.1007/s10584-014-1256-3

Meynard, C.N., Quinn, J.F., 2008. Bird metacommunities in temperate South American forest: Vegetation structure, area, and climate effects. Ecology 89, 981–990. https://doi.org/10.1890/07-0350.1

Milán, M.J., González, E., 2022. Beef–cattle ranching in the Paraguayan Chaco: typological approach to a livestock frontier. Environ. Dev. Sustain. https://doi.org/10.1007/s10668-022-02261-2

Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, V., Gordon, J.E., 2006. A global overview of the conservation status of tropical dry forests. J. Biogeogr. 33, 491–505. https://doi.org/10.1111/j.1365-2699.2005.01424.x

Moreno, M.L., Bernaschini, M.L., Pérez-Harguindeguy, N., Valladares, G., 2014. Area and edge effects on leaf-litter decomposition in a fragmented subtropical dry forest. Acta Oecologica 60, 26–29. https://doi.org/10.1016/j.actao.2014.07.002

Navarro, G., Molina, J.A., Vega, S., 2011. Soil factors determining the change in forests between dry and wet Chacos. Flora Morphol. Distrib. Funct. Ecol. Plants 206, 136–143. https://doi.org/10.1016/j.flora.2010.09.002

Nori, J., Torres, R., Lescano, J.N., Cordier, J.M., Periago, M.E., Baldo, D., 2016. Protected areas and spatial conservation priorities for endemic vertebrates of the Gran Chaco, one of the most threatened ecoregions of the world. Divers. Distrib. 22, 1212–1219. https://doi.org/10.1111/ddi.12497

Páez, S.A., Marco, D.E., 2000. Seedling habitat structure in dry Chaco forest (Argentina). J. Arid Environ. 46, 57–68. https://doi.org/10.1006/jare.2000.0648

Parker III, T.A., Stotz, D.F., Fitzpatrick, J.W., 1996. Ecological and Distributional Databases for Neotropical Birds. University of Chicago Press, Chicago.

Pearson, D.L., 1971. Vertical Stratification of Birds in a Tropical Dry Forest Author (s): David L . Pearson Published by : Oxford University Press Stable URL : https://www.jstor.org/stable/1366123 REFERENCES Linked references are available on JSTOR for this article : You m. Condor 73, 46–55.

Pennington, T.R., Prado, D.E., Pendry, C.A., 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. J. Biogeogr. 27, 261–273. https://doi.org/10.1046/j.1365-2699.2000.00397.x

Pérez-Granados, C., Traba, J., 2021. Estimating bird density using passive acoustic monitoring: a review of methods and suggestions for further research. Ibis (Lond. 1859). https://doi.org/10.1111/ibi.12944

Pérez-Hernández, C.G., Vergara, P.M., Saura, S., Hernández, J., 2015. Do corridors promote connectivity for bird-dispersed trees? The case of Persea lingue in Chilean fragmented landscapes. Landsc. Ecol. 30, 77–90. https://doi.org/10.1007/s10980-014-0111-2

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., Butchart, S.H.M., Arroyo-Rodríguez, V., Barlow, J., Cerezo, A., Cisneros, L., D’Cruze, N., Faria, D., Hadley, A., Harris, S.M., Klingbeil, B.T., Kormann, U., Lens, L., Medina-Rangel, G.F., Morante-Filho, J.C., Olivier, P., Peters, S.L., Pidgeon, A., Ribeiro, D.B., Scherber, C., Schneider-Maunoury, L., Struebig, M., Urbina-Cardona, N., Watling, J.I., Willig, M.R., Wood, E.M., Ewers, R.M., 2017. Creation of forest edges has a global impact on forest vertebrates. Nature 551, 187–191. https://doi.org/10.1038/nature24457

Pijanowski, B.C., Villanueva-Rivera, L.J., Dumyahn, S.L., Farina, A., Krause, B.L., Napoletano, B.M., Gage, S.H., Pieretti, N., 2011. Soundscape ecology: The science of sound in the landscape. Bioscience 61, 203–216. https://doi.org/10.1525/bio.2011.61.3.6

Pollock, H.S., Cheviron, Z.A., Agin, T.J., Brawn, J.D., 2015. Absence of microclimate selectivity in insectivorous birds of the Neotropical forest understory. Biol. Conserv. 188, 116–125. https://doi.org/10.1016/j.biocon.2014.11.013

Portillo-Quintero, C.A., Sánchez-Azofeifa, G.A., 2010. Extent and conservation of tropical dry forests in the Americas. Biol. Conserv. 143, 144–155. https://doi.org/10.1016/j.biocon.2009.09.020

Prado, D.E., Gibbs, P.E., 1993. Patterns of species distributions in the Dry Seasonal Forests of South America. Missouri Bot. Gard. Press 80, 902–927.

R Core Team, 2021. R: A language and environment for statistical computing [WWW Document]. R Found. Stat. Comput. URL http://www.r-project.org/

Rahbek, C., 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecol. Lett. 8, 224–239. https://doi.org/10.1111/j.1461-

0248.2004.00701.x

Remsen, J., Robinson, S., 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Stud. Avian Biol.

Ribeiro, J.R., Las-Casas, F.M.G., Silva, W.A. de G. e, Naka, L.N., 2021. Managed logging negatively affects the density and abundance of some dry forest specialist bird species of northeastern Brazil. Ornithol. Appl. 123, 1–14. https://doi.org/10.1093/ornithapp/duab026

Rodriguez, P., Giménez, R., Nosetto, M.D., Jobbágy, E.G., Magliano, P.N., 2020. Changes in water fluxes partition related to the replacement of native dry forests by crops in the Dry Chaco. J. Arid Environ. 183. https://doi.org/10.1016/j.jaridenv.2020.104281

Roque, F.D.O., Menezes, J.F.S., Northfield, T., Ochoa-Quintero, J.M., Campbell, M.J., Laurance, W.F., 2018. Warning signals of biodiversity collapse across gradients of tropical forest loss. Sci. Rep. 8, 1–7. https://doi.org/10.1038/s41598-018-19985-9

Ruggiero, A., Kitzberger, T., 2004. Environmental correlates of mammal species richness in South America: Effects of spatial structure, taxonomy and geographic range. Ecography (Cop.). 27, 401–417. https://doi.org/10.1111/j.0906-7590.2004.03801.x

Sekercioglu, Ç.H., Ehrlich, P.R., Daily, G.C., Aygen, D., Goehring, D., Sandí, R.F., 2002. Disappearance of insectivorous birds from tropical forest fragments. Proc. Natl. Acad. Sci. U. S. A. 99, 263–267. https://doi.org/10.1073/pnas.012616199

Semper-Pascual, A., Macchi, L., Sabatini, F.M., Decarre, J., Baumann, M., Blendinger, P.G., Gómez-Valencia, B., Mastrangelo, M.E., Kuemmerle, T., 2018. Mapping extinction debt highlights conservation opportunities for birds and mammals in the South American Chaco. J. Appl. Ecol. 55, 1218–1229. https://doi.org/10.1111/1365-2664.13074

Siyum, Z.G., 2020. Tropical dry forest dynamics in the context of climate change: syntheses of drivers, gaps, and management perspectives. Ecol. Process. 9. https://doi.org/10.1186/s13717-020-00229-6

Sodhi, N.S., Smith, K.G., 2007. Conservation of tropical birds: Mission possible? J. Ornithol. 148, 305–309. https://doi.org/10.1007/s10336-007-0180-y

Song, X.-P., Hansen, M.C., Stehman, S. V., Potapov, P. V., Tyukavina, A., Vermote, E.F., Townshend, J.R., 2018. Global land change from 1982 to 2016. Nature. https://doi.org/10.1038/s41586-018-0411-9

Sueur, J., Aubin, T., Simons, C., 2008. Seewave, a free modular tool for sound analysis and synthesis. Bioacoustics 18, 213–226. https://doi.org/10.1080/09524622.2008.9753600

Sueur, J., Farina, A., Gasc, A., Pieretti, N., Pavoine, S., 2014. Acoustic indices for biodiversity assessment and landscape investigation. Acta Acust. united with Acust. 100, 772–781. https://doi.org/10.3813/AAA.918757

Sugai, L.S.M., Silva, T.S.F., Ribeiro, J.W., Llusia, D., 2019. Terrestrial Passive Acoustic Monitoring: Review and Perspectives. Bioscience 69, 5–11. https://doi.org/10.1093/biosci/biy147

Tabarelli, M., Peres, C.A., Melo, F.P.L., 2012. The “few winners and many losers” paradigm revisited: Emerging prospects for tropical forest biodiversity. Biol. Conserv. 155, 136–140. https://doi.org/10.1016/j.biocon.2012.06.020

Tewksbury, J.J., Levey, D.J., Haddad, N.M., Sargent, S., Orrock, J.L., Weldon, A., Danielson, B.J., Brinkerhoff, J., Damschen, E.I., Townsend, P., 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. Proc. Natl. Acad. Sci. U. S. A. 99, 12923–12926. https://doi.org/10.1073/pnas.202242699

Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S., Packer, C., 2017. Future threats to biodiversity and pathways to their prevention. Nature 546, 73–81. https://doi.org/10.1038/nature22900

Vallejos, M., Volante, J.N., Mosciaro, M.J., Vale, L.M., Bustamante, M.L., Paruelo, J.M., 2015. Transformation dynamics of the natural cover in the Dry Chaco ecoregion: A plot level geo-database from 1976 to 2012. J. Arid Environ. 123, 3–11. https://doi.org/10.1016/j.jaridenv.2014.11.009

Vandewalle, M., de Bello, F., Berg, M.P., Bolger, T., Dolédec, S., Dubs, F., Feld, C.K., Harrington, R., Harrison, P.A., Lavorel, S., da Silva, P.M., Moretti, M., Niemelä, J., Santos, P., Sattler, T., Sousa, J.P., Sykes, M.T., Vanbergen, A.J., Woodcock, B.A., 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. Biodivers. Conserv. 19, 2921–2947. https://doi.org/10.1007/s10531-010-9798-9

Villanueva-Rivera, L.J., Pijanowski, B.C., Doucette, J., Pekin, B., 2011. A primer of acoustic analysis for landscape ecologists. Landsc. Ecol. 26, 1233–1246. https://doi.org/10.1007/s10980-011-9636-9

Villard, M.A., Kurtis Trzcinski, M., Merriam, G., 1999. Fragmentation effects on forest birds: Relative influence of woodland cover and configuration on landscape occupancy. Conserv. Biol. 13, 774–783. https://doi.org/10.1046/j.1523-1739.1999.98059.x

Walther, B.A., 2002. Vertical stratification and use of vegetation and light habitats by Neotropical forest birds. J. für Ornithol. 143, 64–81. https://doi.org/10.1007/bf02465460

Walther, G., Post, E., Convey, P., Menzel, A., Parmesank, C., Beebee, T.J.C., Fromentin, J., I, O.H., Bairlein, F., 2002. Ecological response to recent climate cnahge. Nature 416, 389–395.

Werneck, F.P., 2011. The diversification of eastern South American open vegetation biomes: Historical biogeography and perspectives. Quat. Sci. Rev. 30, 1630–1648. https://doi.org/10.1016/j.quascirev.2011.03.009

Whittaker, R.J., Willis, K.J., Field, R., 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. J. Biogeogr. 28, 453–470.

Wiens, J.A., 1999. Habitat fragmentation: island v landscape perspectives on bird conservation, NCASI Technical Bulletin.

Woodworth, B.K., Norris, D.R., Graham, B.A., Kahn, Z.A., Mennill, D.J., 2018. Hot temperatures during the dry season reduce survival of a resident tropical bird. Proc. R. Soc. B Biol. Sci. 285. https://doi.org/10.1098/rspb.2018.0176

Zelaya, P. V., Blendinger, P.G., Palacio, F.X., Marinaro, S., Macchi, L., Gasparri, N.I., 2022. Above-ground biomass and high temperatures are more important than productivity for the spatial pattern of bird richness in Subtropical Dry forests of Argentina. Community Ecol. 23, 41–54. https://doi.org/10.1007/s42974-021-00071-6

Zimbres, B., Peres, C.A., Machado, R.B., 2017. Terrestrial mammal responses to habitat structure and quality of remnant riparian forests in an Amazonian cattle-ranching landscape. Biol. Conserv. 206, 283–292. https://doi.org/10.1016/j.biocon.2016.11.033

Supporting Information for:

Bird communities in the Dry Chaco of South America: vegetation structure and climate effects

Fig 1A. Canonical correspondence analysis (CCA) to select uncorrelated variables: basal area density, understory density, canopy density, canopy openness for vegetation structure, temperature (TP), and wind speed (WS), relative humidity (RH) for climate factors.

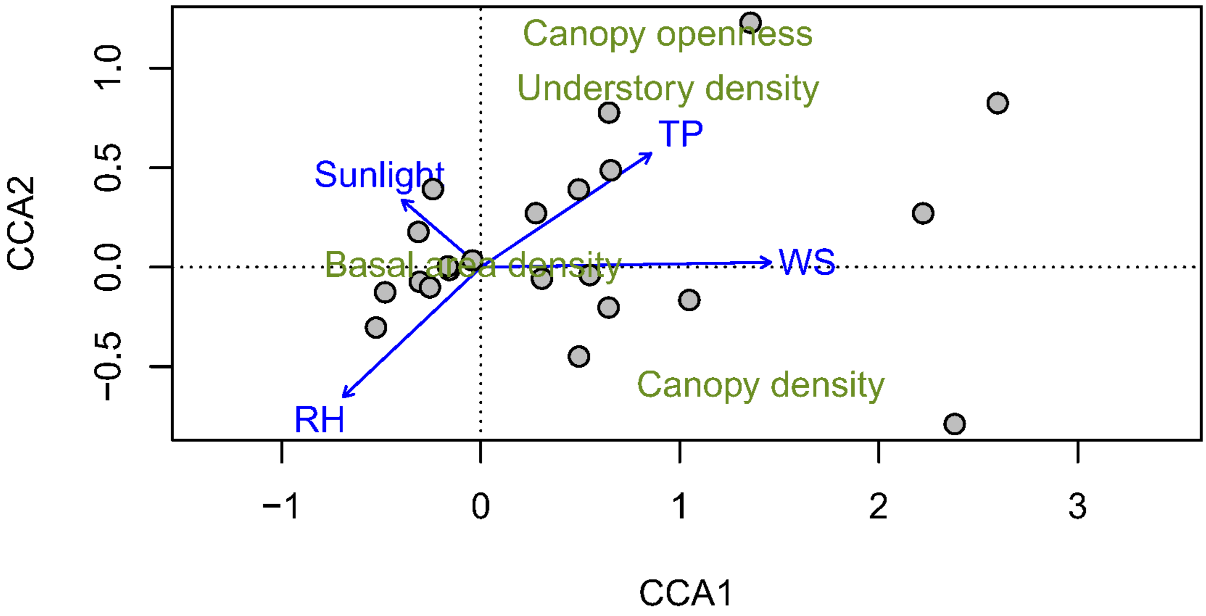


Fig A2. The Non-Metric Multidimensional Scaling (NMDS) ordination plot the dissimilarity of bird communities within two different agricultural land cover, anthropological region and agriculture frontier contexts based on Bray-Curtis's index.

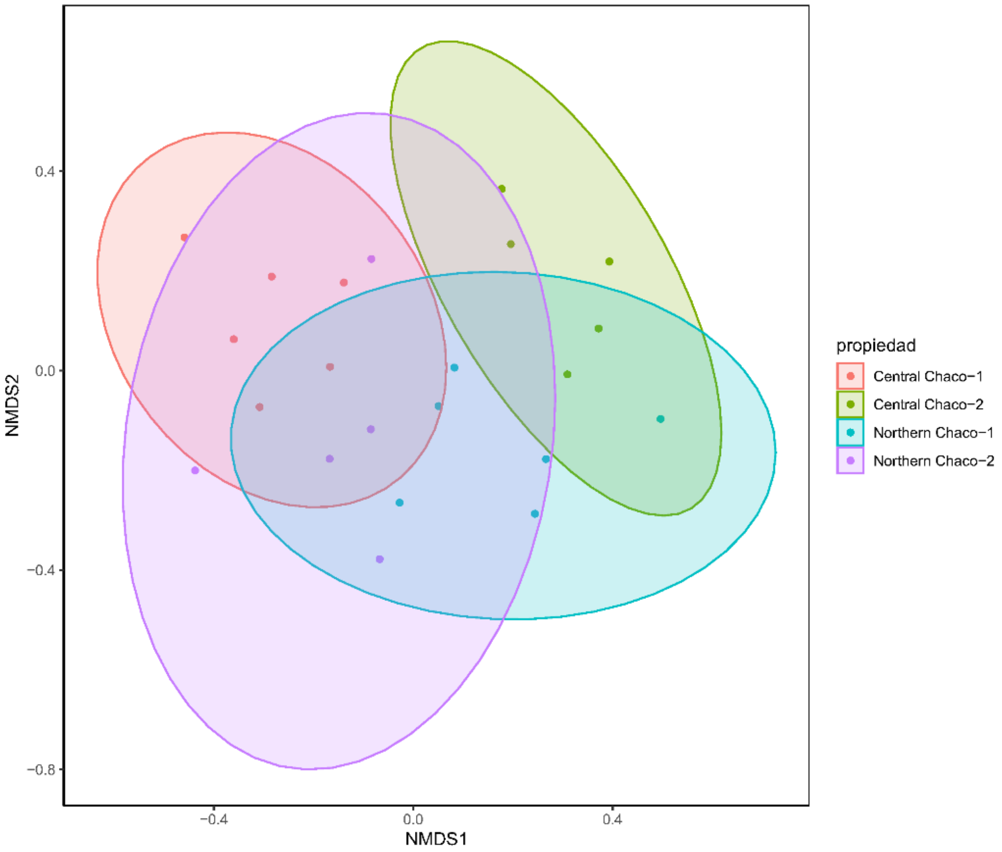


Table S1. Birds identified at the 22 forest corridors of the Paraguayan Chaco. Birds were categorized as tropical dry forest restricted from 1 (frequently occurring in other habitats such as tropical rain forest) to 3 (restricted to tropical dry forest, and strongly avoiding other habitats), following Dardanelli et al (2006), Semper-Pascual et al. (2018), Parker et al. (1996) and distribution maps on Birds of the world (https://birdsoftheworld.org/).

Species	**Restricted to dry forest**
Amazona aestiva	1
Ammodramus humeralis	1
Aratinga nenday	3
Asthenes baeri	2
Cacicus solitarius	1
Campephilus leucopogon	3
Campylorhamphus trochilirostris	1
Caracara plancus	1
Cariama cristata	1
Casiornis rufus	1
Chunga burmeisteri	3
Colaptes melanochloros	1
Columbina squammata	1
Columbina talpacoti	1
Coryphistera alaudina	3
Cranioleuca pyrrhophia	2
Crypturellus tataupa	3
Cyanocorax chrysops	1
Cyclarhis gujanensis	1
Drymornis bridgesii	3
Dryobates mixtus	2
Euphonia chlorotica	1
Furnarius cristatus	3
Furnarius rufus	1
Glaucidium brasilianum	1
Guira guira	1

Heliomaster furcifer	1
Hemitriccus margaritaceiventer	1
Herpetotheres cachinnans	1
Icterus croconotus	1
Icterus pyrrhopterus	1
Inezia inornata	2
Knipolegus striaticeps	3
Lepidocolaptes angustirostris	1
Leptotila verreauxi	1
Lophospingus pusillus	3
Megascops choliba	1
Melanerpes cactorum	3
Melanerpes candidus	1
Melanopareia maximilliani	3
Microspingus melanoleucus	3
Molothrus bonariensis	1
Myiarchus tyrannulus	1
Myiopsitta monachus	1
Myrmorchilus strigilatus	3
Nothoprocta cinerascens	3
Nothura maculosa	1
Nystalus maculatus	2
Ortallis canicollis	3
Paroaria coronata	1
Patagioenas picazuro	1
Phacellodomus sibilatrix	3
Picumnus cirratus	1
Pitangus sulphuratus	1
Polioptila dumicola	1
Pseudoscops clamator	1
Pseudoseisura lophotes	2
Rhinocrypta lanceolata	3
Rupornis magnirostris	1

Saltator aurantirostris	2
Saltatricula multicolor	3
Schoeniophylax phryganophilus	2
Setopagis parvula	1
Setophaga pitiayumi	1
Sittasomus griseicapillus	1
Stigmatura burytoides	3
Strix chacoensis	3
Sublegatus modestus	2
Suiriri suiriri	2
Synallaxis frontalis	2
Tapera naevia	1
Taraba major	1
Thamnophilus caerulescens	1
Thamnophilus doliatus	1
Thectocercus acuticaudatus	2
Troglodytes aedon	1
Turdus amaurochalinus	1
Tyto alba	1
Vireo olivaceus	1
Xiphocolaptes major	3

Table S2. Results of the Multi Response Permutation Procedure (MRPP) and the values of two axes of the Non-metric Multidimensional Scaling (NMDS) for all birds. Temperature (TP), and wind speed (WS), relative humidity (RH)

Environmental variables	NMDS1	NMDS2	pval
Basal area density	0.008536	-0.20779	0.655
Understory.density	-0.31834	-0.10006	0.327
Canopy.oppeness	-0.39494	0.373442	0.034
Canopy.density	0.516964	-0.17321	0.039
Sunlight	0.116186	0.243389	0.463
WS	0.507112	0.066474	0.056
TP	0.195624	0.542983	0.025
RH	-0.05976	-0.58089	0.016

Table S3. Results of the Multi Response Permutation Procedure (MRPP) and the values of two axes of the Non-metric Multidimensional Scaling (NMDS) for dry-forest birds. Temperature (TP), and wind speed (WS), relative humidity (RH).

Environmental variables	NMDS1	NMDS2	pval
Basal area density	0.236284	0.130303714	0.483
Understory.density	-0.38352	0.055554036	0.221
Canopy.oppeness	-0.42939	0.072865382	0.129
Canopy.density	0.687303	0.213955966	0.001
Sunlight	-0.00012	0.132520206	0.828
WS	0.450503	-0.290861326	0.041
TP	-0.00685	-0.023659017	0.992
RH	0.036751	0.124200122	0.857

Table S4. Results of the indicator species analysis (ISA) and the values of the two axes of the Non-metric Multidimensional Scaling (NMDS) for all birds.

Species	NMDS1	NMDS2	pval
A.aestiva	-0.12492	0.439855	0.104
A.humeralis	-0.66631	0.023248	0.006
A.nenday	0.262331	0.503146	0.006
A.baeri	-0.43297	0.249222	0.066
C.solitarius	0.12089	0.294168	0.342
C.leucopogon	0.243869	0.1211	0.527
C.trochilirostris	-0.41219	0.53283	0.003
C.plancus	0.246503	-0.0116	0.718
C.cristata	-0.44842	-0.28012	0.026
C.rufus	0.578809	-0.39084	0.002
C.burmeisteri	-0.02819	-0.54796	0.043
C.melanochloros	0.246503	-0.0116	0.718
C.squammata	0.110565	0.089525	0.843
C.talpacoti	-0.05144	0.309788	0.37
C.alaudina	-0.33303	-0.01491	0.316
C.pyrrhophia	-0.43548	0.497886	0.004
C.tataupa	-0.38453	-0.38487	0.021
C.chrysops	0.409273	0.074424	0.15
C.gujanensis	0.62631	0.389905	0.001
D.bridgesii	0.169634	0.190284	0.524
D.mixtus	-0.08624	0.205218	0.823
E.chlorotica	0.15796	0.522069	0.038
F.cristatus	-0.44186	0.412287	0.013
F.rufus	0.080251	-0.13548	0.779
G.brasilianum	0.116504	-0.04996	0.859
G.guira	0.020824	-0.29911	0.432
H.furcifer	-0.45846	0.143823	0.084
H.margaritaceiventer	-0.57574	0.382161	0.005
H.cachinnans	0.258872	0.236661	0.305

I.croconotus	0.065468	0.314557	0.385
I.pyrrhopterus	-0.04948	0.148937	0.798
I.inornata	0.465214	0.457111	0.004
K.striaticeps	0.097894	0.61652	0.01
L.angustirostris	0.32888	0.231786	0.17
L.verreauxi	0.509562	0.236468	0.035
L.pusillus	0.32434	0.219124	0.183
M.choliba	0.520535	-0.16717	0.025
M.cactorum	-0.04981	0.248847	0.713
M.candidus	0.055957	-0.02278	0.96
M.maximilliani	0.007256	0.157421	0.768
M.melanoleucus	-0.24126	0.458918	0.066
M.bonariensis	0.165622	0.27708	0.364
M.tyrannulus	0.011376	-0.46723	0.096
M.monachus	-0.15215	0.226342	0.475
M.strigilatus	0.067416	0.084189	0.882
N.cinerascens	-0.48065	-0.01518	0.077
N.maculosa	-0.22905	-0.49276	0.012
N.maculatus	-0.30344	-0.49734	0.015
O.canicollis	-0.74832	0.343053	0.001
P.coronata	0.503312	0.312067	0.01
P.picazuro	-0.08138	-0.03836	0.929
P.sibilatrix	-0.50178	-0.04332	0.064
P.cirratus	0.246503	-0.0116	0.718
P.sulphuratus	0.294507	0.397171	0.085
P.dumicola	0.268829	0.222788	0.277
P.clamator	-0.04981	0.248847	0.713
P.lophotes	0.292792	-0.3637	0.099
R.lanceolata	-0.26354	0.398954	0.03
R.magnirostris	0.384537	-0.14114	0.234
S.aurantirostris	-0.07646	0.330888	0.3
S.multicolor	-0.06549	0.213069	0.61
S.phryganophilus	-0.19735	-0.23832	0.357

S.parvula	0.193603	-0.45326	0.08
S.pitiayumi	-0.08806	0.490315	0.054
S.griseicapillus	-0.05238	-0.1359	0.878
S.burytoides	-0.63084	0.318372	0.003
S.chacoensis	-0.4507	-0.14597	0.079
S.modestus	-0.11332	0.000863	0.88
S.suiriri	0.234526	0.288363	0.265
S.frontalis	0.118646	0.110646	0.804
T.naevia	-0.13287	0.011309	0.902
T.major	-0.31075	-0.6351	0.002
T.caerulescens	0.007112	0.642096	0.006
T.doliatus	-0.47663	0.123793	0.065
T.acuticaudatus	0.018283	0.216204	0.648
T.aedon	0.250512	-0.22854	0.335
T.amaurochalinus	-0.02022	0.133508	0.837
T.alba	0.17945	-0.2248	0.598
V.olivaceus	-0.15952	0.270353	0.402
X.major	-0.26039	0.170773	0.389

Table S5. Results of the indicator species analysis (ISA) and the values of two axes of the Non-metric Multidimensional Scaling (NMDS) for dry-forest birds.

Species	NMDS1	NMDS2	pval
A.nenday	-0.0474	0.687659	0.006
C.leucopogon	0.154915	-0.3755	0.175
C.burmeisteri	0.285926	0.135393	0.359
C.alaudina	0.028789	-0.42948	0.167
C.tataupa	-0.33427	-0.00974	0.318
D.bridgesii	0.225418	-0.13723	0.495
F.cristatus	-0.31411	-0.14523	0.332
K.striaticeps	0.095018	0.792825	0.001
L.pusillus	0.11993	0.567954	0.02
M.cactorum	-0.19559	-0.28461	0.365
M.maximilliani	-0.28057	0.347875	0.132
M.melanoleucus	-0.22995	0.546758	0.02
M.strigilatus	-0.40804	0.557159	0.006
N.cinerascens	-0.66736	-0.31292	0.001
O.canicollis	-0.50724	-0.32257	0.02
P.sibilatrix	-0.37734	-0.08526	0.194
R.lanceolata	-0.07155	0.15462	0.739
S.multicolor	-0.03468	-0.07432	0.968
S.burytoides	-0.43544	-0.03601	0.142
S.chacoensis	-0.23804	0.177765	0.378
X.major	-0.1351	-0.22639	0.501

Table S6. Best-performing models output examining the relationship between variables measuring vegetation structure and climate variables for the communities of all birds and dry-birds only. Model selection results, detailed the ΔAICc < 2 set of models

Response variable	Models	Best (fit) models	df	AICc	delta	weight
Dry-forest birds	Basal area density + Canopy density + Understory density + Temperature + Wind speed	Understory density	20	102.48	0.00	0.131
		Canopy density	20	104.02	1.54	0.060
		Understory density + Canopy density	19	104.04	1.56	0.060
All birds	Basal area density + Canopy density + Understory density + Temperature + Wind speed	Temperature	2	126.59	0	0.390

Table S7. Set of models output from GLMM models examining temperature effects for the communities of all birds.

All birds				
Response variable	Predictor variable	Estimate	SD	Pr(Chi)
ADI	Intercept	2.245067	0.070165	
	Temperature	-0.005350	0.002783	0.05559
BI	Intercept	7.34940	0.91700	0.6234
	Temperature	-0.02365	0.03726	

Capítulo 4

Acoustic indices as a rapid assessment of bird communities in the Dry Chaco, South America

Abstract

Agricultural expansion led to negative impacts on biodiversity around the world. Regions with high human pressure, rapidly occupied, and extensively understudied, like the Dry Chaco in South America, require rapid studies to understand the environmental impacts and potential loss of biodiversity. Ecoacoustics could be an efficient method to promote rapid assessment in threatened regions. Using a unique field-based bird community dataset, we evaluate the performance of two acoustic indices (acoustic diversity index and acoustic complexity index) on the representation of avian richness in continuous forest and forest corridors of the Paraguayan Dry Chaco. Our analyses revealed that acoustic indices poorly explained overall avian richness variation, including continuous forest and forest corridors. However, when analyzing bird communities in continuous forest and forest corridors, acoustic indices reflected changes in avian richness along the latter. Furthermore, the acoustic indices captured differences between the regions, with small values for forest corridors and higher for the continuous forest. Overall, our study adds to an incipient field suggesting that acoustic indices were sensitive to landscape complexity and the importance of evaluating their efficacy and limitations under different conditions and environmental dissimilarities. Likewise, our study highlights the need to use acoustic indices as a potential rapid assessment, supported by species richness analyses to help the acoustic indices interpretation.

Keywords: passive acoustic method, ecoacoustics, avian richness, landscape structure, bird monitoring

Introduction

Biodiversity has been degraded in many parts of the world and a key driver is habitat destruction due to agricultural expansion and intensification (Tilman *et al.* 2017). This is particularly relevant in the tropics and subtropics, where agriculture continues to expand into remaining natural areas (Lambin and Meyfroidt 2011; Song et al. 2018), which harbor high and unique biodiversity (Laurance et al. 2014; Roque et al. 2018). Agricultural expansion and biodiversity losses are most drastic in the tropics, yet ecological and conservation science has a solid prevailing bias to focus on land-use impacts on biodiversity outside the tropics (Trimble and van Aarde 2012; Martin *et al.* 2012). As a result, our understanding of the impacts of agricultural land-use change on biodiversity is partial for many regions.

Tropical and sub-tropical dry forests (hereafter: tropical dry forests or TDF) are widespread and provide essential ecosystem services, including carbon sequestration, while holding unique biodiversity (Siyum 2020; Pennington *et al.* 2018). Unfortunately, many TDF are threatened due to agricultural expansion (Buchadas *et al.* 2022; Davis *et al.* 2020) and defaunation (Pennington *et al.* 2018; Dirzo *et al.* 2014). In addition to the human pressures, most TDF remain under-researched (Pennington *et al.* 2018) and weakly protected (Pimm et al. 2014), translating into barriers to effective conservation planning and action (Miles *et al.* 2006). This is particularly the case for South America, where less than 10% of TDF remain with little or no human pressure (Pennington *et al.* 2018; Escribano-Avila *et al.* 2017; Portillo-Quintero and Sánchez-Azofeifa 2010). There is an urgent need to understand how biodiversity responds to the increasing human pressure on South America’s dry forests. The Gran Chaco is the largest dry forest ecoregion in South America and has recently been hard-hit by agricultural expansion. Widespread soybean and cattle ranching expansion have turned this region into a global deforestation hotspot (Hansen *et al.* 2013; Song *et al.* 2018; Kuemmerle *et al.* 2017). Within the Chaco, deforestation has been rampant in Paraguay since 2010 (Baumann *et al.* 2017; de la Sancha *et al.* 2021).

The habitat loss in the Chaco urges the adoption of rapid and effective methods for monitoring its biodiversity. An emerging field of monitoring biodiversity is soundscape ecology, which can be defined as the study of the spatial-temporal patterns and processes resulting from an interaction of existing sounds in a landscape with biodiversity and the human being (Pijanowski *et al.* 2011). Landscape sounds can be divided into sounds emitted by animals (biophony), by geophysical (geophony), and by humans (anthrophony or technophony) (Krause 1987). Bioacoustics is part of such field (Sueur *et al.* 2008), as well as the new emerging ecoacoustic (Sueur and Farina 2015). Both bioacoustics and ecoacoustics focus on studying biological sound behavior, although ecoacoustic introduces ecological and biodiversity conservation issues. Data collecting is a non-invasive method, and it helps estimate biodiversity activity and occurrence (Hill *et al.* 2018) while minimizing human disturbance and interferences and allows for long-term monitoring of a wide range of vocal species (Sugai et al. 2019; Pérez-Granados and Traba 2021). Among other advantages, the methods allow for large-scale surveys with multiple sites sampled simultaneously. The data processing and analytical tools increased in recent years, including automatic and semi-automatic methods for proper identification (Sugai *et al.* 2019; Pijanowski *et al.* 2011; Pieretti *et al.* 2015). Although bioacoustics is an increasing discipline worldwide, it is biased toward urban areas and temperate regions, disregarding Neotropics threats (Scarpelli *et al.* 2020).

Acoustic indices represent automatic analyses used in biodiversity and ecological studies (Sueur *et al.* 2014; Kasten *et al.* 2012; Pieretti *et al.* 2015). The automatic analyses provide faster results, an excellent method for rapid assessments that save hours or days to identify the recorded species. Acoustic indices are mathematical functions designed to represent biodiversity, reflecting species richness, abundance, and evenness, among other community characteristics in a given time and space (Sueur *et al.* 2014; Pieretti and Farina 2013). Some of the most used acoustic indices include the Acoustic Complexity Index (ACI), which is based in differences on intensities of biotic sounds along time (Pieretti and Farina 2013; Pieretti *et al.* 2011). It results from the change in spectral amplitude with the average frequency of the full recording. The Acoustic Diversity Index (ADI) is calculated based on Shannon entropy (Villanueva-Rivera *et al.* 2011), and the Bioacoustic Index (BI) was designed to capture all sound across the frequencies range (Boelman et al. 2007). The acoustic entropy index (H) is calculated based on temporal and spectral entropies. Temporal entropies refer to time units and their frequencies within a recording, and spectral entropies refer to the energy through the spectrum, followed by the Shannon index application (Sueur *et al.* 2008). The acoustic evenness index (AEI) is calculated based on the Gini coefficient, which reflects the occupancy at each frequency band per recording (Villanueva-Rivera *et al.* 2011). Finally, the normalized difference soundscape index (NDSI) computes the anthrophony level of human-generated compared to biophony of biological-generated (Kasten *et al.* 2012).

Tropical birds are an interesting focus group for understanding the effects of habitat loss and fragmentation on biodiversity. Likewise, birds are good indicators of landscape change, as many have clear habitat associations, responding quickly to environment changes (Gregory *et al.* 2005; Vandewalle *et al.* 2010). Some species are more sensitive to habitat loss and fragmentation, especially those forest depended, therefore affected by reduce the populations' size and sometimes leading them on a trajectory toward local extinction (Hanski 1998; Wiens 1999). The most common methods of the avian community included traditional active point-count surveys. In general, birds are audible species with characteristic vocal sounds. Acoustic indices convert bird signatures to assess the spatial and temporal distributions of different birds in ecosystems (Pijanowski *et al.* 2011). This method is helpful for quick assessments, reduces the time of processing records, and can be associated with species diversity or species activity, providing a rapidly assessed biodiversity (Sueur *et al.* 2008; Pijanowski *et al.* 2011). Several studies correlate audible species with acoustic diversity (e.g., Machado et al. 2017; Mammides et al. 2017), including bird activities (Pieretti *et al.* 2011; Pérez-Granados and Traba 2021; Pieretti and Farina 2013; Boelman *et al.* 2007). Then, the acoustic indices may represent bird diversity well enough to help in more automatic and rapid monitoring.

A few studies had performed automatic analyses to investigate birds responses in dry lands of the Neotropics (Oliveira *et al.* 2021; Owen *et al.* 2020; Hilje *et al.* 2017), and none were developed in the Chaco, which has undergone the most drastic forest loss recently. Within the Chaco region, deforestation has been most rampant in the Paraguayan Chaco since 2010 (Baumann *et al.* 2022; Vallejos *et al.* 2015; Hansen *et al.* 2013). We used automatic recorder devices to characterize bird communities' richness in two distinct regions of the Paraguayan Chaco dry forest (continuous forest and corridors) and to compare them using acoustic indices. Several laws in Paraguay were designed to protect natural vegetation and forest resources. Properties larger than 100 ha are requested by Decree 18,831/86 (Milán and González 2022) to maintain forested areas at least 100 m wide between agricultural plots, named "windbreaks", which has the primary objective of restraining the wind pressure and avoiding erosions. Although no study shows the importance of such strips in promoting biodiversity protection, they indubitably contribute to maintaining the structural connectivity of the landscape. Thus, such strips should hold part of the local biodiversity, even temporarily, representing an excellent opportunity to conduct ecological studies.

We tested the hypothesis that acoustic indices are associated with bird activity in the Paraguayan Chaco. First, we predicted that acoustic indices would reflect the characteristics of bird communities in terms of activity and richness. Second, we predicted that such association is observed in continuous forest and forest corridors.

Materials and methods

Study area

The Gran Chaco is a biogeographic region comprising the Wet Chaco and Dry Chaco. The Dry Chaco is the largest tropical dry forest in South America, extending over a flat terrain over an area of 840,000 km² in Argentina, Paraguay, and Bolivia. The Dry Chaco contains a mosaic of xerophytic vegetation formations, including dry forests, scrublands, and savannas (Pennington *et al.* 2000; Werneck 2011). The soils in the Chaco are mainly based on fluvial pedogenesis in the north and derive from eolic sediments and loess material in the south (Navarro *et al.* 2011). The climate is semiarid, with summer maxima of up to 49 °C. There is a strong east-west rainfall gradient (450–700 mm) and marked seasonality, with a dry season in the winter/spring and a rainy season in the summer/autumn. Vegetation can be subjected to low soil moisture and freezing temperatures during the dry season and waterlogging and extremely high temperatures during the rainy season (Pennington *et al.* 2000).

The Paraguayan Chaco (Figure 1) is a region where natural vegetation is dominated by xeromorphic forest and scrubland (Mereles and Rodas 2014). Most of the natural vegetation has a low level of protection, with only 16.2% of the original area included in protected areas (Nori *et al.* 2016). The region is rapidly converted to agriculture by domestic and international agribusiness actors who establish large farms mainly for producing beef for international markets (Baumann *et al.* 2022; Franco-Solís and Montanía 2021; Milán and González 2022). Despite the general trend, the Paraguayan Chaco contains diverse deforestation dynamics. Deforestation in the central Paraguayan Chaco leads to small and isolated fragments of remaining forests (Mereles and Rodas 2014). In contrast, larger blocks of natural vegetation remain in the landscape in the northern Paraguayan Chaco, where the agricultural frontier currently expand (Vallejos *et al.* 2015). Furthermore, properties larger than 100 ha must maintain strips of forests at least 100 m wide between agricultural plots (Decree 18,831/86). Such strips are locally named “cortinas” (a Spanish word for windbreaks) and aim to restrain the north wind pressure and avoid erosions. The windbreaks, hereafter referred to as forest corridors, give singularity to the Paraguayan Chaco landscape.

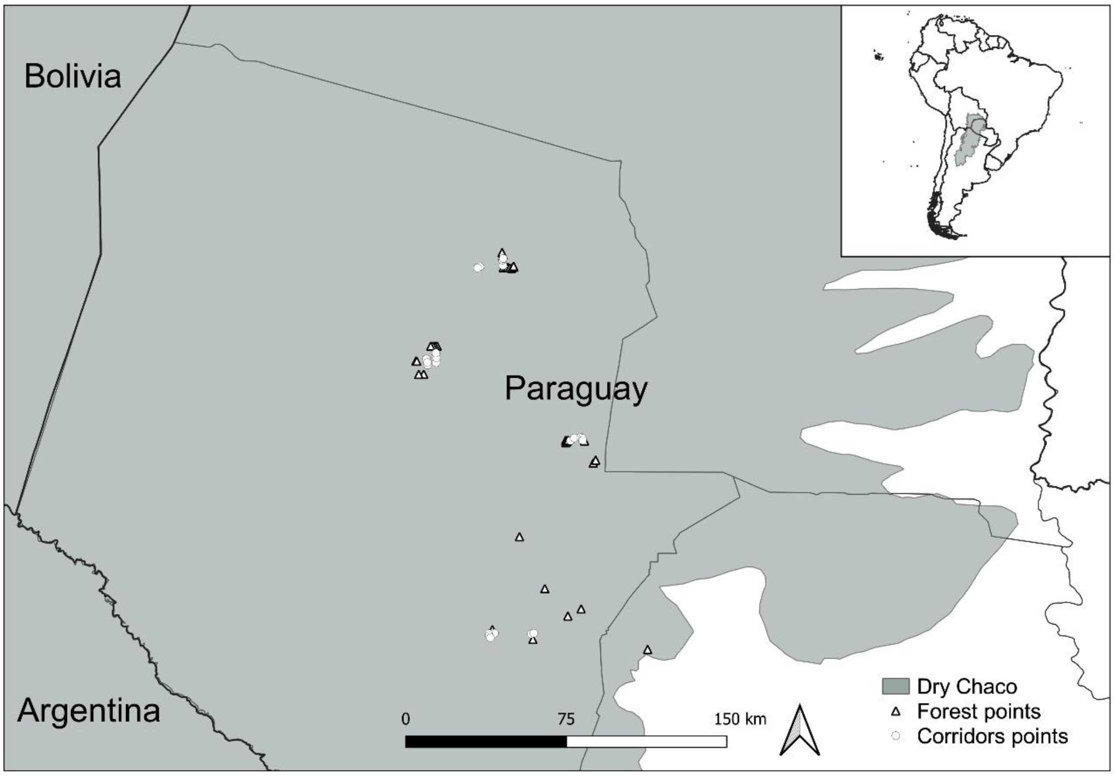


Figure 1. Study area in the Paraguayan Dry Chaco with the 56 sampling points, 34 points at the continuous forest (white triangle) and 22 points at the forest corridors (white circle), delimited with a gray line is the Dry Chaco of South America.

Bird surveys

We used automatic sound recorders (Audiomoth from Open Acoustics Devices) to sample bird communities. We surveyed birds in 56 sites (34 in continuous forest and 22 in forest corridors), all located inside larger cattle ranches. Sites were selected based on landscape characteristics to include diverse landscape configurations in both the central and northern Paraguayan Chaco. We installed recorders at 2-meter-height in trees separated by at least 500 meters between sites, considering the recording scope (Hill *et al.* 2018).

We recorded two days at each site in September and October of 2019, coinciding with the end of the dry season, a period when most birds in this region initiate breeding. Each recording consisted of 10-minute samples (wave format, 48 MHz of sampling rate, monophonic, and 16 bits) during the peak of avian vocal activity (i.e., 05:00 to 08:30 a.m.

in the morning and 06:00 to 07:00 p.m.) to detect both diurnal and nocturnal birds. The recording had intervals of 10 min between each file.

Data analysis

We analyzed the recordings manually and automatically. Bird species were identified manually by the same person (R.C.), listening to the recordings helped by the stereo spectrogram program Raven Pro 1.6 (Center for Conservation Bioacoustics 2019). We only registered persistent singing and excluded songs of flying birds (e.g., songs of flying parrots) and used bird's songs repository for species identification (Xeno-Canto, www.xeno- canto.org; and Macaulay Library www.macaulaylibrary.org), as well as consulting with experts on bird songs from the region.

We performed automatic analyses to calculate the acoustic indices. We calculated six acoustic indices (Acoustic Complexity Index – ACI, Acoustic Diversity Index – ADI, Acoustic Evenness – AEI, Bioacoustic Index – BI, Total Entropy – H, and Normalized Difference Soundscape Index – NDSI). We selected the most representative hours of the day for both continuous forest and corridors to include the period with the most activity and to avoid wind interference. We selected 14 recordings (10-min each) per site and split the file into one-minute duration samples to calculate the acoustic indices. Thus, we analyzed 7,840 files with the packages *soundecology* (Villanueva-Rivera *et al.* 2011) and the *seewave* (Sueur *et al.* 2008) in R (R Core Team 2021).

Statistical analysis

We performed a descriptive analysis to inspect the variables (Figure S1, S2). We used the median values based on 7,840 recordings of each acoustic index. ADI, ACI, and BI showed significant variation across the sites. Then rank a correlation to evaluate the associations between them. We selected three AI to avoid correlation and because they represented our objectives best: ADI, ACI, and BI (Figure S3). We assumed a linear relationship between AI and bird richness for all points and each group (i.e., forest and corridor).

Richness values were not normally distributed (Shapiro test W = 0.851, p = 0.486) as well as for ADI (Shapiro test W = 0.8191, p-value = 8.383e-07), ACI, (Shapiro test W = 0.9576, p-value = 0.04702) and BI (Shapiro test W = 0.94917, p-value = 0.01953) so we used a Wilcoxon test to test for potential differences index between habitats. To evaluate the relationship between AI and bird richness, we constructed a generalized linear model (GLM). AI and richness were logarithmically transformed to avoid the impact of detached observations. All analyzes were performed using R software (R Core Team 2021), and all differences were considered statistically significant for $p < 0.05$.

Results

Richness across our 34 continuous forest points was 99 species for all communities. Eight species (8%) were ubiquitous, occurring in all sites (*Lepidocolaptes angustirostris, Hemitriccus margaritaceiventer, Chunga burmeisteri, Cyclarhis gujanensis, Furnarius cristatus, Myiarchus tyrannulus, Patagioenas picazuro* and *Paroaria coronata*). Richness across our 22 forest corridors was 80 for the entire avian community. Three birds (2.4%) were ubiquitous in all sites, (*Furnarius rufus, Lepidocolaptes angustirostris*, and *Suiriri suiriri)*. From the entire avian community, 22 birds were heard only in the continuous forest, while three birds were heard only in the corridors. We concluded that both habitats have consistent samples effort to use the richness results (Figure S4).

Richness per habitat was significantly higher in continuous forest (mean= 52.0, sd= 6.18) than in corridors (mean= 29.9, sd= 3.83) (Figure 2). The number of birds identified per habitat ranged from 40 to 61 in the continuous forest and 22 to 36 in the forest corridors. Acoustic indices ADI (i.e., ADI continuous forest, mean= 2.16, sd= 0.09, ADI corridor, mean= 2.14, sd= 0.12) and ACI (i.e., ACI continuous forest, mean= 776, sd= 9.96, ACI corridor, mean= 774, sd= 9.64) differences between the habitats were less significant (Figure 2).

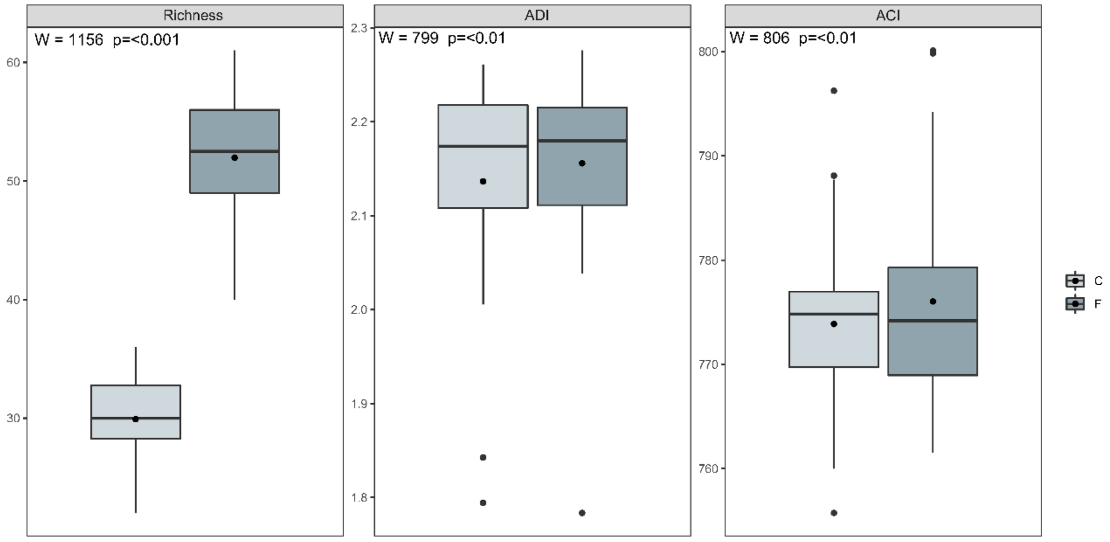


Figure 2. Distribution of the three responses of avian across 34 sampling sites of continuous forest (F) and 22 corridors (C) in the dry forest of the Paraguayan Chaco, for all birds that were recorded (richness) and for the acoustic indices: Acoustic Diversity Index (ADI) and Acoustic Complexity Index (ACI). Box plots show median, quartiles, as well as maximum and minimum values.

The correlation of ADI with the richness of the overall community showed no significant relationships (Figure 3(a)), yet when split into the two habitats, corridors showed a significant positive relationship with richness (Figure 3(b)), although only explained 23% of the variation in birds' communities. Otherwise, ADI was not significant in the continuous forest (Figure 3(b)). The correlation of ACI with the richness of the entire community showed a weak relationship, with only 5% explaining the variations (Figure 3(c)). For the corridors, ACI showed a significant positive relationship with richness (Figure 3(d)), although it only explained 18% of the variation in birds' communities. Otherwise, for the continuous forest, ACI showed weak relationships, with only 8% explaining the variations (Figure 3(d)). The acoustic index BI showed no significant results (Figure S5).

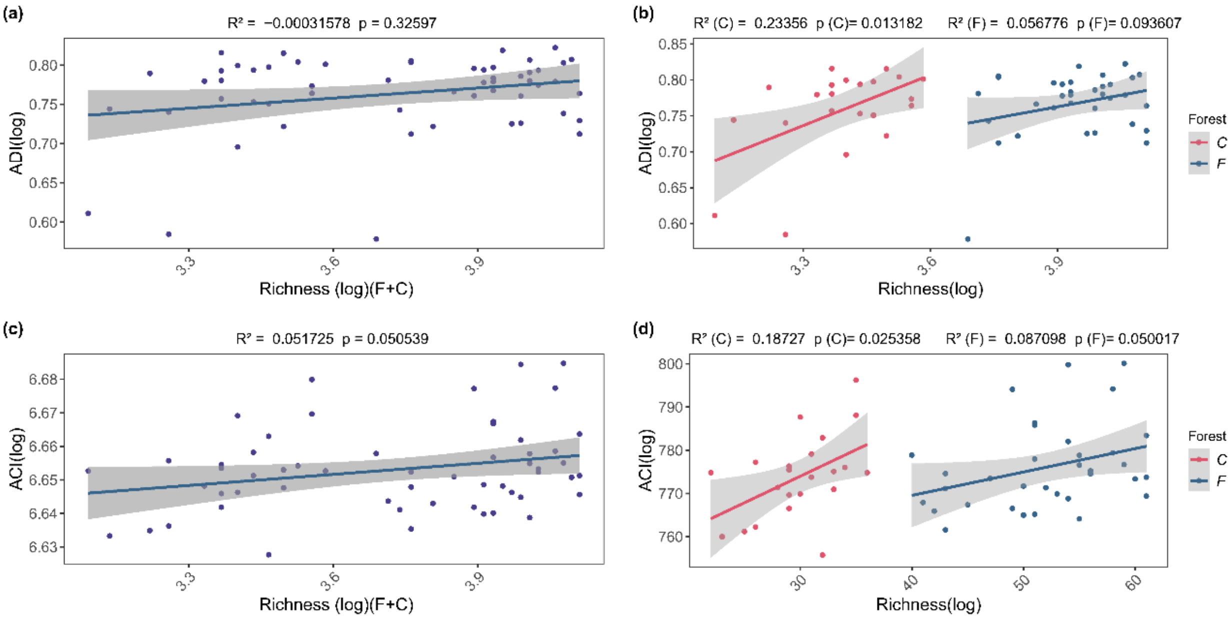


Figure 3. Relationships of the acoustic indices with richness: Acoustic Diversity Index (ADI) (a-b) and Acoustic Complexity Index (ACI) (c-d) in the Paraguayan Chaco. Relationship included the entire community (continuous forest and corridors) (a,c),

corridors (red points) and continuous forest (blue points) (b,d). Shaded areas are 95% confidence intervals.

Discussion

Land use change drives habitat loss and fragmentation worldwide, leading to a diverse deforestation dynamic that affects biodiversity. The Paraguayan Chaco is no exception to this pattern, with the aggravating factor of being one of the world's deforestation hotspots. As a result of high human pressure over the last decades, natural landscapes in the Paraguayan Chaco became a mosaic of continuous forests, fragments, and forest corridors. Bird communities have responded to such pressure, and it is possible to verify a reduction in species diversity. We associated bird communities with the acoustic indices at the Dry Chaco, Paraguay. We showed no correlation when compare the entire community (i.e., bird from the continuous forest and forest corridors) with acoustic indices. This explained differences between bird communities from the two areas, communities of corridors and continuous areas were different and the indices cannot accurate correlations with species richness. Species richness was higher in continuous forest than in forest corridors. This indicates differences between the regions. The acoustic indices explained changes in bird communities at the corridors, yet not at the continuous forest. This evidence that landscape structure should contribute to different characteristics between communities, even at sites with common structure. As far as we know, this is the first study to compare bird communities with acoustic indices at the Dry Chaco.

We found that species richness was higher in the continuous forest than in forest corridors (on average, 52 species for continuous forests and 30 species for corridors). However, there is a wide variation in the species richness per sampling points in the former. We registered a variation of 21 species between the sampled point in continuous forests (minimum of 40 species and maximum of 61), while the variation registered for corridors was 14 species. The weak association between acoustic indices and species richness for continuous forests is due to the high variation in the detected species because we found a significant relationship for the corridors. The association of acoustic indices and species diversity has already been shown for different regions and biomes (e.g., Machado *et al.* 2017; Mammides *et al.* 2017; Oliveira *et al.* 2021), including dry forests (Hilje *et al.* 2017; Oliveira *et al.* 2021) and also for other taxonomic groups (Silva *et al.* 2022), being a valid proxy for the biodiversity. The considerable variation in species richness observed in continuous forests can be related to historic disturbance events. The agricultural frontier tends to expand over large blocks of native vegetation in the Paraguayan Chaco (de la Sancha *et al.* 2021, Kuemmerle *et al.* 2017).

Acoustic indices explained changes in bird communities at the corridors, yet not at the continuous forest (Figure 3(b), (d)). This evidence that landscape structure increases dissimilarities between continuous forest sites offering diverse characteristics to avian communities. The differences between landscape structures in the Paraguayan Chaco constitute evident, containing diverse deforestation dynamics. This included larger blocks of natural vegetation (Vallejos *et al.* 2015) and small and isolated fragments of remaining forests (Mereles and Rodas 2014). Instead, the forest corridors are rectangular elements, surrounded by agricultural plots, and are longer than wide, connected, or not to the continuous forest. Despite that, environmental dissimilarity should affect correlation coefficients between acoustic indices and the avian species richness, but interferences of species other than birds are possible (Mammides *et al.* 2017). The impacts of human occupation caused differences in the landscape structure and should contribute to different characteristics between communities, even at sites with a common structure. As far as we know, this is the first study to compare bird communities with acoustic indices at the Dry Chaco.

Previous studies showed that bird communities responded to differences in landscape structure and forest quality (Herzog and Kessler 2002; Mastrangelo and Gavin 2014; Ocampo-Peñuela and Etter 2013). The continuous forest refers to a greater area, more resources, less edge pressure, able to support a variety of communities with high requirements, such as forest specialists (Wiens 1999; Sodhi and Smith 2007). Even though forest corridors can provide suitable habitats for bird species by increasing the connectivity of forest fragments in the landscape (Gonzalez *et al.* 2010; Lindenmayer and Nix 1993), such areas are very small and exposed to external impacts (isolation, edge effects, nest predation, cattle intrusion, among other) (Wiens 1999; Sodhi and Smith 2007). Differences between continuous forest and forest corridors should be responded to conservation status, affecting the vegetation structure and quality. Most of the continuous forest constitute private legal reserves with low or no direct pressure. Otherwise, corridors are structural elements requested by law to be maintained between agricultural plots without conservation status. Forest corridors continue suffering from external pressure, such as selecting logging, cattle intrusion, firewood, and anthropic fires (Gasparri and Baldi 2013; Ribeiro *et al.* 2021). Such impacts reduce the forest's habitat quality, and afect canopy and understory cover. Finally, studies have suggested that vegetation cover and microclimatic affect species richness and bird species composition (Meynard and Quinn 2008; Gonçalves *et al.* 2017; Loaiza *et al.* 2020).

Our study relied on a unique, field-based bird community dataset using acoustic recorders in the Dry Chaco. Still, we count on some limitations to be mentioned. First, our study period corresponded to the dry season. It is well known that vegetation structure fluctuates in the dry and rainy seasons, gradually increasing or decreasing its complexity and affecting bird activities (Kalacska *et al.* 2005; Woodworth *et al.* 2018). Therefore, future studies should focus on how acoustic indices vary between seasons, including the rainy season. We recommended extending the temporal monitoring to include bird activities with automatic analyses. The automatic analyses facilitate the process and analysis of many recordings. Alternatively, we suggest analyzing how bird communities respond to landscape characteristics (e.g., fragments size and connectivity). Also, considering other habitat characteristics, like habitat degradation as a variable, explained community changes, especially for forest corridors.

Overall, our results showed that acoustic indices have the potential to be used as a valid rapid assessment to study birds of the Dry Chaco yet considering different landscape elements such as continuous forest and forest corridors. Acoustic indices reflect the avian richness responses for corridors but not continuous forests. Importantly, when analyzing both regions, the low correlations suggest some limitations, and acoustic indices may need to be more accurate in the differences in bird communities under these conditions. Consequently, further studies should include the landscape differences in the continuous forest to test the effectiveness of acoustic indices. As the ecoacoustic field is incipient in the Dry Chaco, evaluating their efficacy and limitations is essential under different conditions and environmental dissimilarities. We recommended using acoustic indices (i.e., ADI and ACI) as a potential rapid assessment of environmental impacts in large areas and protected areas, supported by species richness analyses to help the acoustic indices interpretation.

.

Acknowledgements

We are grateful to the Brazilian Ministry of Education (CAPES) for RC's PhD scholarship, and the National Council of Scientific and Technological Development (CNPq) for RBM's fellowship grant. We thank the German Academic Exchange (DAAD-CAPES) and Humboldt-Universität zu Berlin for hosting RC during a research stay. We also thank Rufford Small Grants Foundation (#28259-1) and the Graduate Program in Ecology, University of Brasilia (CAPES/PROEX) for help in the purchase of recordings and the financial support for the fieldwork in the Chaco, Paraguay. We are indebted to Hugo del Castillo and Lucas Cañete for assistance in the fieldwork, and all landowners for granting access to their properties.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Disclosure statement

We have no competing interests to declare

Funding

This work was supported by the Rufford Small Grants Foundation under Grant number 28259-1; and Graduate Program in Ecology – University of Brasilia, CAPES/PROEX under Grant number 0769/2020.

References

Baumann M., Gasparri N. I., Buchadas A. *et al.* (2022) Frontier metrics for a process-based understanding of deforestation dynamics. *Environ. Res. Lett.* doi: 10.1088/1748-9326/ac8b9a.

Baumann M., Israel C., Piquer-Rodríguez M., Gavier-Pizarro G., Volante J. N. & Kuemmerle T. (2017) Deforestation and cattle expansion in the Paraguayan Chaco 1987–2012. *Reg. Environ. Chang.* **17** , 1179–1191.

Bierregaard, R. O., Lovejoy T. E., Kapos V. & Hutchings R. W. (1992) The Biological Dynamics of Tropical Rainforest Fragments. *Bioscience* **42** , 859–866.

Boelman N. T., Asner G. P., Hart P. J. & Martin R. E. (2007) Multi-Trophic invasion resistance in Hawaii: bioacoustics, field surveys, and airborne remote sensing. *Ecol. Appl.* **17** , 2137–2144. [online]. Available from: http://doi.wiley.com/10.1890/07-0004.1.

Buchadas A., Baumann M., Meyfroidt P. & Kuemmerle T. (2022) Uncovering major types of deforestation frontiers across the world's tropical dry woodlands. *Nat. Sustain.* doi: 10.1038/s41893-022-00886-9.

Davis K. F., Koo H. I., Dell'Angelo J. *et al.* (2020) Tropical forest loss enhanced by large-scale land acquisitions. *Nat. Geosci.* **13** , 482–488. [online]. Available from: http://dx.doi.org/10.1038/s41561-020-0592-3.

Dirzo R., Young H. S., Galetti M., Ceballos G., Isaac N. J. B. & Collen B. (2014) Defaunation in the Anthropocene. *Science (80-.).* **345** , 401–406.

Escribano-Avila G., Cervera L., Ordóñez-Delgado L. *et al.* (2017) Biodiversity patterns and ecological processes in Neotropical dry forest: the need to connect research and management for long-term conservation. *Neotrop. Biodivers.* **3** , 107–116. [online]. Available from: https://doi.org/10.1080/23766808.2017.1298495.

Franco-Solís A. & Montanía C. V. (2021) Dynamics of deforestation worldwide: A structural decomposition analysis of agricultural land use in South America. *Land use policy* doi: 10.1016/j.landusepol.2021.105619. [online]. Available from: https://doi.org/10.1016/j.landusepol.2021.105619.

Gasparri N. I. & Baldi G. (2013) Regional patterns and controls of biomass in semiarid woodlands: Lessons from the Northern Argentina Dry Chaco. *Reg. Environ. Chang.* **13** , 1131–1144.

Gonçalves G. S. R., Cerqueira P. V., Brasil L. S. & Santos M. P. D. (2017) The role of climate and environmental variables in structuring bird assemblages in the Seasonally Dry Tropical Forests (SDTFs). *PLoS One* **12** , 1–16.

Gonzalez P., Neilson R. P., Lenihan J. M. & Drapek R. J. (2010) Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. *Glob. Ecol. Biogeogr.* **19** , 755–768.

Gregory R. D., Van Strien A., Vorisek P. *et al.* (2005) Developing indicators for European birds. *Philos. Trans. R. Soc. B Biol. Sci.* **360** , 269–288.

Hansen M. C., Potapov P. V, Moore R. *et al.* (2013) High-resolution global maps of 21st-century forest cover change. *Science* **342** , 850–3. [online]. Available from: http://www.ncbi.nlm.nih.gov/pubmed/24233722.

Hanski I. (1998) Metapopulation dynamics. *Nature* **396** , 41–49.

Herzog S. K. & Kessler M. (2002) Biogeography and composition of dry forest bird communities in Bolivia. *J. fur Ornithol.* **143** , 171–204.

Hilje B., Stack S. & Sánchez-Azofeifa A. (2017) Lianas abundance is positively related with the avian acoustic community in tropical dry forests. *Forests* **8** , 1–12.

Hill A. P., Prince P., Piña Covarrubias E., Doncaster C. P., Snaddon J. L. & Rogers A. (2018) AudioMoth: Evaluation of a smart open acoustic device for monitoring biodiversity and the environment. *Methods Ecol. Evol.* **9** , 1199–1211.

Kalacska M. E. R., Sánchez-Azofeifa G. A., Calvo-Alvarado J. C., Rivard B. & Quesada M. (2005) Effects of season and successional stage on leaf area index and spectral vegetation indices in three mesoamerican tropical dry forests. *Biotropica* **37** , 486–496.

Kasten E. P., Gage S. H., Fox J. & Joo W. (2012) The remote environmental assessment laboratory's acoustic library: An archive for studying soundscape ecology. *Ecol. Inform.* doi: 10.1016/j.ecoinf.2012.08.001. [online]. Available from: http://dx.doi.org/10.1016/j.ecoinf.2012.08.001.

Krause B. (1987) Whole Earth. *Whole Earth* , 142p.

Kuemmerle T., Baldi G., Camino M. *et al.* (2017) Forest conservation : Remember Gran Chaco Forest conservation : Humans ' handprints. *Science (80-.).* **355** , 465–467.

de la Sancha N. U., Boyle S. A., McIntyre N. E. *et al.* (2021) The disappearing Dry Chaco, one of the last dry forest systems on earth. *Landsc. Ecol.* **36** , 2997–3012.

Lambin E. F. & Meyfroidt P. (2011) Global land use change, economic globalization, and the looming land scarcity. *Proc. Natl. Acad. Sci. U. S. A.* **108** , 3465–3472.

Laurance W. F., Sayer J. & Cassman K. G. (2014) Agricultural expansion and its impacts on tropical nature. *Trends Ecol. Evol.* **29** , 107–116. [online]. Available from: http://dx.doi.org/10.1016/j.tree.2013.12.001.

Lindenmayer D. B. & Nix H. A. (1993) Ecological Principles for the Design of Wildlife Corridors. *Conserv. Biol.* **7** , 627–631.

Loaiza C., Montenegro O. L., King D., Spínola M., Palacio L. A. & Rudas A. (2020) Variation in abundance and habitat relationship of three understory insectivorous birds in a disturbed landscape of Neotropical dry forest of Colombia. *Avian Res.* **11** , 1–12. [online]. Available from: https://doi.org/10.1186/s40657-020-00219-4.

Machado R. B., Aguiar L. & Jones G. (2017) Do acoustic indices reflect the characteristics of bird communities in the savannas of Central Brazil? *Landsc. Urban Plan.* doi: 10.1016/j.landurbplan.2017.01.014.

Mammides C., Goodale E., Dayananda S. K., Kang L. & Chen J. (2017) Do acoustic indices correlate with bird diversity? Insights from two biodiverse regions in Yunnan Province, south China. *Ecol. Indic.* **82** , 470–477. [online]. Available from: http://dx.doi.org/10.1016/j.ecolind.2017.07.017.

Martin L. J., Blossey B. & Ellis E. (2012) Mapping where ecologists work: Biases in the global distribution of terrestrial ecological observations. *Front. Ecol. Environ.*

10 , 195–201.

Mastrangelo M. E. & Gavin M. C. (2014) Impacts of agricultural intensification on avian richness at multiple scales in Dry Chaco forests. *Biol. Conserv.* doi: 10.1016/j.biocon.2014.08.020. [online]. Available from: http://linkinghub.elsevier.com/retrieve/pii/S0006320714003103.

Mereles M. F. & Rodas O. (2014) Assessment of rates of deforestation classes in the Paraguayan Chaco (Great South American Chaco) with comments on the vulnerability of forests fragments to climate change. *Clim. Change* **127** , 55–71. [online]. Available from: http://link.springer.com/10.1007/s10584-014-1256-3 [Accessed November 20, 2014].

Meynard C. N. & Quinn J. F. (2008) Bird metacommunities in temperate South American forest: Vegetation structure, area, and climate effects. *Ecology* **89** , 981–990.

Milán M. J. & González E. (2022) Beef–cattle ranching in the Paraguayan Chaco: typological approach to a livestock frontier. *Environ. Dev. Sustain.* [online]. Available from: https://doi.org/10.1007/s10668-022-02261-2.

Miles L., Newton A. C., DeFries R. S. *et al.* (2006) A global overview of the conservation status of tropical dry forests. *J. Biogeogr.* **33** , 491–505.

Navarro G., Molina J. A. & Vega S. (2011) Soil factors determining the change in forests between dry and wet Chacos. *Flora Morphol. Distrib. Funct. Ecol. Plants* **206** , 136–143. [online]. Available from: http://linkinghub.elsevier.com/retrieve/pii/S0367253010001118.

Nori J., Torres R., Lescano J. N., Cordier J. M., Periago M. E. & Baldo D. (2016) Protected areas and spatial conservation priorities for endemic vertebrates of the Gran Chaco, one of the most threatened ecoregions of the world. *Divers. Distrib.* **22** , 1212–1219.

Ocampo-Peñuela N. & Etter A. (2013) Contribution of Different Forest Types To the Bird Community of a Savanna Landscape in Colombia. *Ornitol. Neotrop.* **24** , 35–53.

Oliveira E. G., Ribeiro M. C., Roe P. & Sousa-Lima R. S. (2021) The Caatinga Orchestra: Acoustic indices track temporal changes in a seasonally dry tropical forest. *Ecol. Indic.* doi: 10.1016/j.ecolind.2021.107897. [online]. Available from: https://doi.org/10.1016/j.ecolind.2021.107897.

Owen K. C., Melin A. D., Campos F. A., Fedigan L. M., Gillespie T. W. & Mennill D.

J. (2020) Bioacoustic analyses reveal that bird communities recover with forest succession in tropical dry forests. *Avian Conserv. Ecol.* **15** , 1–20.

Pennington R. T., Lehmann C. E. R. & Rowland L. M. (2018) Tropical savannas and dry forests. *Curr. Biol.* **28** , R541–R545. [online]. Available from: http://dx.doi.org/10.1016/j.cub.2018.03.014.

Pennington T. R., Prado D. E. & Pendry C. A. (2000) Neotropical seasonally dry forests and Quaternary vegetation changes. *J. Biogeogr.* **27** , 261–273. [online]. Available from: http://doi.wiley.com/10.1046/j.1365-2699.2000.00397.x.

Pérez-Granados C. & Traba J. (2021) Estimating bird density using passive acoustic monitoring: a review of methods and suggestions for further research. *Ibis (Lond. 1859).*. **163**, 765–783.

Pieretti N., Duarte M. H. L., Sousa-Lima R. S., Rodrigues M., Young R. J. & Farina A. (2015) Determining temporal sampling schemes for passive acoustic studies in different tropical ecosystems. *Trop. Conserv. Sci.* **8** , 215–234.

Pieretti N. & Farina A. (2013) Application of a recently introduced index for acoustic complexity to an avian soundscape with traffic noise. *J. Acoust. Soc. Am.* **134** , 891–900.

Pieretti N., Farina A. & Morri D. (2011) A new methodology to infer the singing activity of an avian community: The Acoustic Complexity Index (ACI). *Ecol. Indic.* **11** , 868–873. [online]. Available from: http://dx.doi.org/10.1016/j.ecolind.2010.11.005.

Pijanowski B. C., Villanueva-Rivera L. J., Dumyahn S. L. *et al.* (2011) Soundscape ecology: The science of sound in the landscape. *Bioscience* **61** , 203–216.

Portillo-Quintero C. A. & Sánchez-Azofeifa G. A. (2010) Extent and conservation of tropical dry forests in the Americas. *Biol. Conserv.* **143** , 144–155. [online]. Available from: http://dx.doi.org/10.1016/j.biocon.2009.09.020.

R Core Team (2021) R: A language and environment for statistical computing. *R Found. Stat. Comput.* [online]. Available from: http://www.r-project.org/.

Ribeiro J. R., Las-Casas F. M. G., Silva W. A. de G. e & Naka L. N. (2021) Managed logging negatively affects the density and abundance of some dry forest specialist bird species of northeastern Brazil. *Ornithol. Appl.* **123** , 1–14.

Roque F. D. O., Menezes J. F. S., Northfield T., Ochoa-Quintero J. M., Campbell M. J. & Laurance W. F. (2018) Warning signals of biodiversity collapse across gradients of tropical forest loss. *Sci. Rep.* **8** , 1–7. [online]. Available from:

http://dx.doi.org/10.1038/s41598-018-19985-9.

Scarpelli M. D. A., Ribeiro M. C., Teixeira F. Z., Young R. J. & Teixeira C. P. (2020) Gaps in terrestrial soundscape research: It's time to focus on tropical wildlife. *Sci. Total Environ.* doi: 10.1016/j.scitotenv.2019.135403. [online]. Available from: https://doi.org/10.1016/j.scitotenv.2019.135403.

Silva C. de A., Machado R. B., Silveira M. & Aguiar L. M. S. (2022) Listening in the dark: acoustics indices reveal bat species diversity in a tropical savannah. *Bioacoustics* **00** , 1–16. [online]. Available from: https://doi.org/10.1080/09524622.2022.2053741.

Siyum Z. G. (2020) Tropical dry forest dynamics in the context of climate change: syntheses of drivers, gaps, and management perspectives. *Ecol. Process.* **9**.

Sodhi N. S. & Smith K. G. (2007) Conservation of tropical birds: Mission possible? *J. Ornithol.* **148** , 305–309.

Song X.-P., Hansen M. C., Stehman S. V. *et al.* (2018) Global land change from 1982 to 2016. *Nature* doi: 10.1038/s41586-018-0411-9. [online]. Available from: http://www.nature.com/articles/s41586-018-0411-9.

Sueur J., Aubin T. & Simons C. (2008) Seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics* **18** , 213–226. [online]. Available from: https://www.tandfonline.com/doi/full/10.1080/09524622.2008.9753600.

Sueur J. & Farina A. (2015) Ecoacoustics: the Ecological Investigation and Interpretation of Environmental Sound. *Biosemiotics* **8** , 493–502.

Sueur J., Farina A., Gasc A., Pieretti N. & Pavoine S. (2014) Acoustic indices for biodiversity assessment and landscape investigation. *Acta Acust. united with Acust.* **100** , 772–781.

Sueur J., Pavoine S., Hamerlynck O. & Duvail S. (2008) Rapid Acoustic Survey for Biodiversity Appraisal (ed D. Reby). *PLoS One* **3** , e4065. [online]. Available from: https://dx.plos.org/10.1371/journal.pone.0004065.

Sugai L. S. M., Silva T. S. F., Ribeiro J. W. & Llusia D. (2019) Terrestrial Passive Acoustic Monitoring: Review and Perspectives. *Bioscience* **69** , 5–11.

Tilman D., Clark M., Williams D. R., Kimmel K., Polasky S. & Packer C. (2017) Future threats to biodiversity and pathways to their prevention. *Nature* **546** , 73–81.

Trimble M. J. & van Aarde R. J. (2012) Geographical and taxonomic biases in research on biodiversity in human-modified landscapes. *Ecosphere* **3** , art119.

Vallejos M., Volante J. N., Mosciaro M. J., Vale L. M., Bustamante M. L. & Paruelo J.

M. (2015) Transformation dynamics of the natural cover in the Dry Chaco ecoregion: A plot level geo-database from 1976 to 2012. *J. Arid Environ.* **123** , 3–11. [online]. Available from: https://linkinghub.elsevier.com/retrieve/pii/S0140196314002420.

Vandewalle M., de Bello F., Berg M. P. *et al.* (2010) Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodivers. Conserv.* **19** , 2921–2947.

Villanueva-Rivera L. J., Pijanowski B. C., Doucette J. & Pekin B. (2011) A primer of acoustic analysis for landscape ecologists. *Landsc. Ecol.* **26** , 1233–1246.

Werneck F. P. (2011) The diversification of eastern South American open vegetation biomes: Historical biogeography and perspectives. *Quat. Sci. Rev.* **30** , 1630–1648. [online]. Available from: http://dx.doi.org/10.1016/j.quascirev.2011.03.009.

Wiens J. A. (1999) *Habitat fragmentation: island v landscape perspectives on bird conservation*.

Woodworth B. K., Norris D. R., Graham B. A., Kahn Z. A. & Mennill D. J. (2018) Hot temperatures during the dry season reduce survival of a resident tropical bird. *Proc. R. Soc. B Biol. Sci.* **285**.

Supporting Information for:

Acoustic indices as a rapid assessment to monitoring bird communities in the Dry Chaco, South America

Table S1. Bird species identified at the Paraguayan Dry Chaco from 56 sampling points set on the continuous forest and corridors gallery forest. We used recordings devices to identified birds (see Methods for details).

Especie	Continuous forest	Corridor
Nothura maculosa		x
Eudromia formosa	x	
Crypturellus undulatus	x	
Crypturellus tataupa	x	x
Nothoprocta cinerascens	x	x
Ortalis canicollis	x	x
Patagioenas picazuro	x	x
Leptotila verreauxi	x	x
Columbina squammata		x
Zenaida auriculata	x	
Columbina picui	x	
Columbina talpacoti		x
Guira guira	x	x
Tapera naevia	x	x
Nyctibius griseus	x	
Setopagis parvula	x	x
Chaetura meridionalis	x	
Heliomaster furcifer	x	x
Chlorostilbon lucidus	x	
Vanellus chilensis	x	
Theristicus caudatus	x	
Buteogallus urubitinga	x	
Rupornis magnirostris	x	x
Tyto alba	x	x
Megascops choliba	x	x
Strix chacoensis	x	x
Glaucidium brasilianum	x	x
Pseudoscops clamator	x	x
Nystalus maculatus	x	x

Picumnus cirratus	x	x
Melanerpes candidus	x	x
Melanerpes cactorum	x	x
Dryobates mixtus	x	x
Campephilus leucopogon	x	x
Dryocopus schulzii	x	
Colaptes melanochloros	x	x
Cariama cristata	x	x
Chunga burmeisteri	x	x
Herpetotheres cachinnans	x	x
Caracara plancus	x	x
Myiopsitta monachus	x	x
Amazona aestiva	x	x
Aratinga nenday	x	x
Thectocercus acuticaudatus	x	x
Psittacara leucophthalmus	x	
Taraba major	x	x
Thamnophilus doliatus	x	x
Thamnophilus caerulescens	x	x
Myrmorchilus strigilatus	x	x
Melanopareia maximiliani	x	x
Rhinocrypta lanceolata	x	x
Sittasomus griseicapillus	x	x
Xiphocolaptes major	x	x
Campylorhamphus trochilirostris	x	x
Drymornis bridgesii	x	x
Lepidocolaptes angustirostris	x	x
Furnarius rufus	x	x
Furnarius cristatus	x	x

Phacellodomus sibilatrix	x	x
Coryphistera alaudina	x	x
Asthenes baeri	x	x
Cranioleuca pyrrhophia	x	x
Pseudoseisura lophotes	x	x
Schoeniophylax phryganophilus	x	x
Synallaxis frontalis	x	x
Camptostoma obsoletum	x	
Suiriri suiriri	x	x
Serpophaga subcristata	x	
Stigmatura budytoides	x	x
Sublegatus modestus	x	x
Inezia inornata	x	x
Hemitriccus margaritaceiventer	x	x
Lathrotriccus euleri	x	
Knipolegus striaticeps	x	x
Machetornis rixosa	x	
Pitangus sulphuratus	x	x
Tyrannus melancholicus	x	
Casiornis rufus	x	x
Myiarchus tyrannulus	x	x
Cyclarhis gujanensis	x	x
Vireo olivaceus	x	x
Cyanocorax chrysops	x	x
Troglodytes aedon	x	x
Polioptila dumicola	x	x
Turdus rufiventris	x	
Turdus amaurochalinus	x	x
Ammodramus humeralis	x	x
Zonotrichia capensis	x	
Euphonia chlorotica	x	x

Cacicus solitarius	x	x
Icterus croconotus	x	x
Icterus pyrrhopterus	x	x
Molothrus bonariensis	x	x
Setophaga pitiayumi	x	x
Sicalis flaveola	x	
Saltatricula multicolor	x	x
Saltator coerulescens	x	
Saltator aurantiirostris	x	x
Microspingus melanoleucus	x	x
Lophospingus pusillus	x	x
Paroaria capitata	x	
Paroaria coronata	x	x

Figure S1. Acoustic indices values along the continuous forest points to inspect the variation across the sites. Acoustic Complexity Index - ACI, Acoustic Diversity Index - ADI, Acoustic Evenness - AEI, Bioacoustic Index - BI, Total Entropy - H, and Normalized Difference Soundscape Index - NDSI

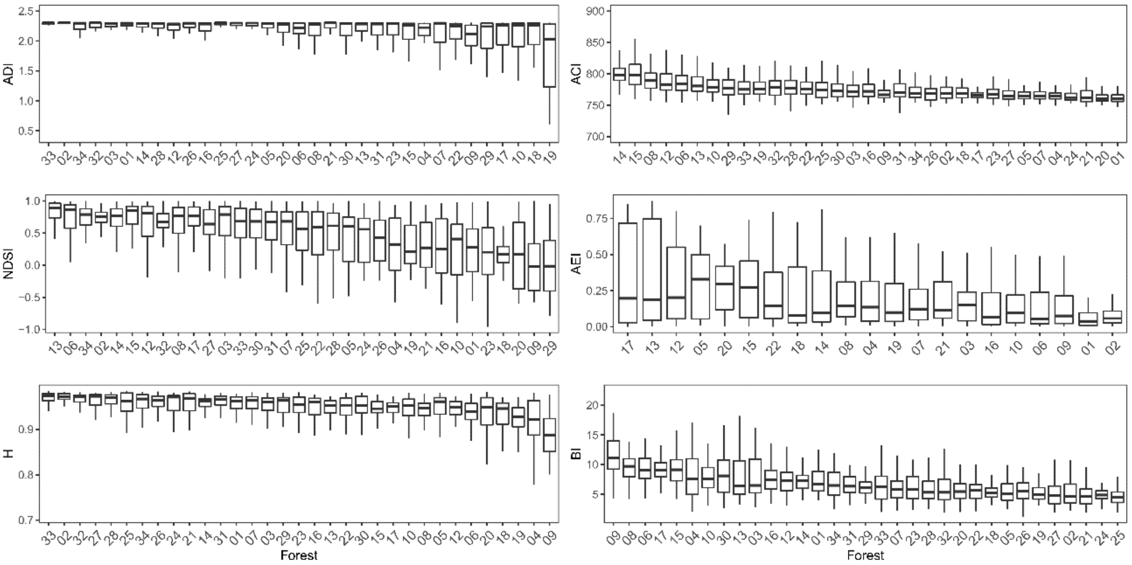


Figure S2. Acoustic indices values along the corridors points to inspect the variation across the sites. Acoustic Complexity Index - ACI, Acoustic Diversity Index - ADI, Acoustic Evenness - AEI, Bioacoustic Index - BI, Total Entropy - H, and Normalized Difference Soundscape Index - NDSI

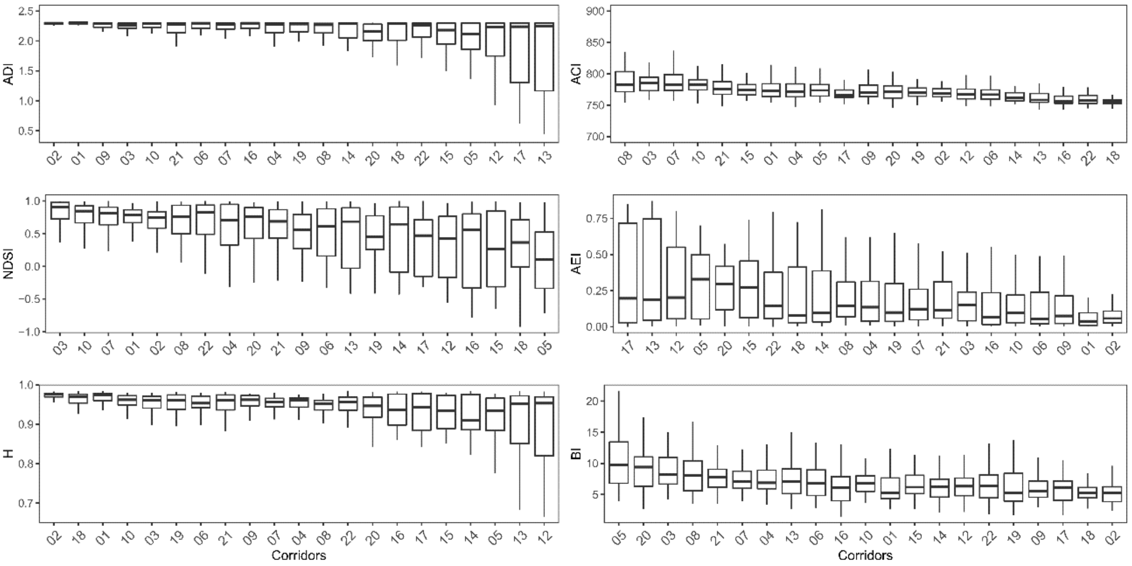


Figure S3. Spearman rank correlation between six acoustic indices used. Acoustic Complexity Index - ACI, Acoustic Diversity Index - ADI, Acoustic Evenness - AEI, Bioacoustic Index - BI, Total Entropy - H, and Normalized Difference Soundscape Index - NDSI

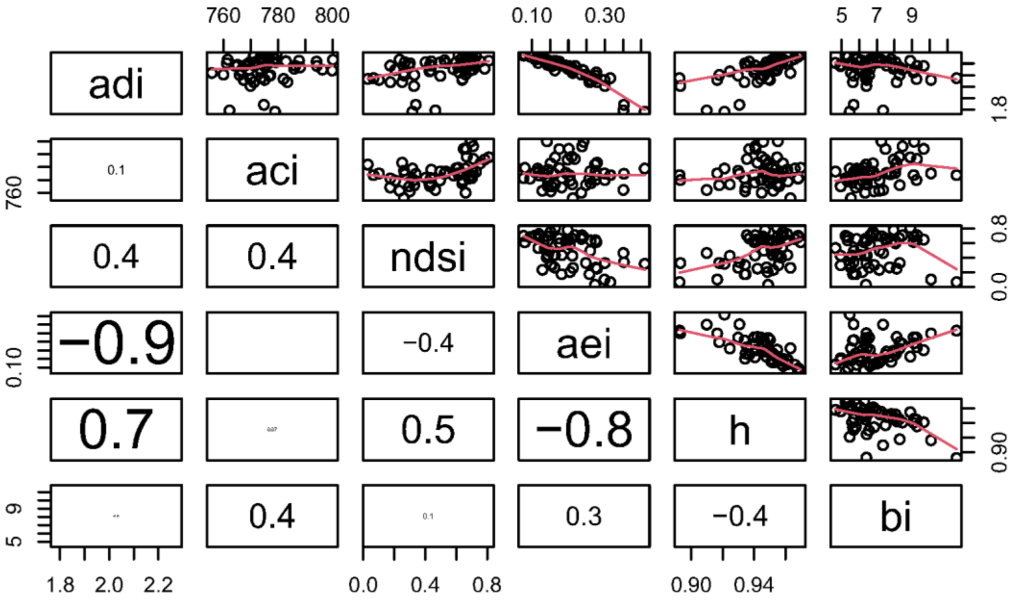


Figure S4. Rarefaction results comparing species diversity and samples efforts at the 34 sites of continuous forest (a) and 22 sites of corridors (b).

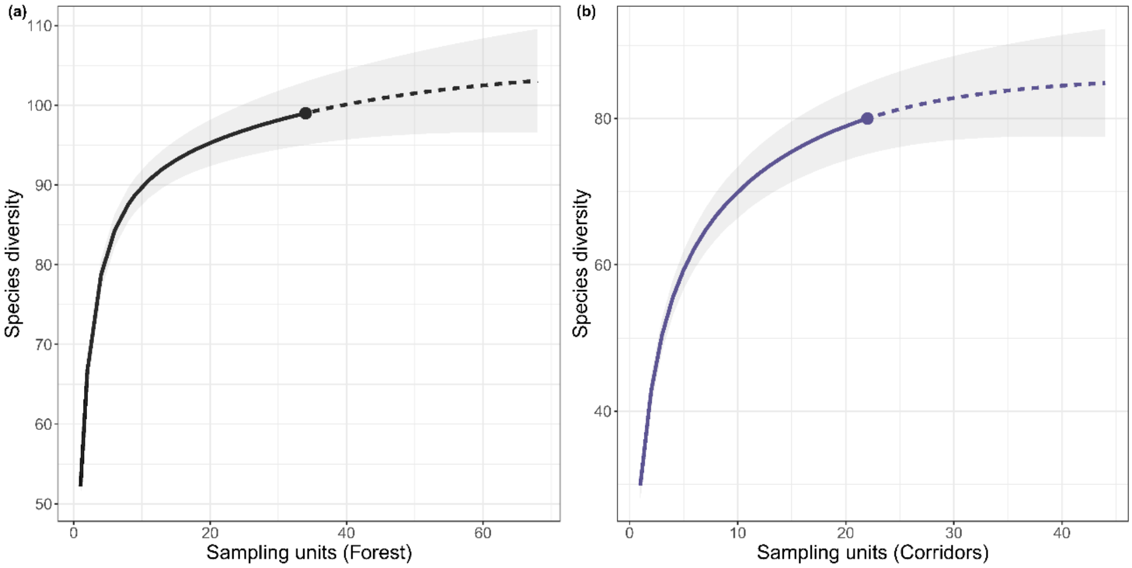
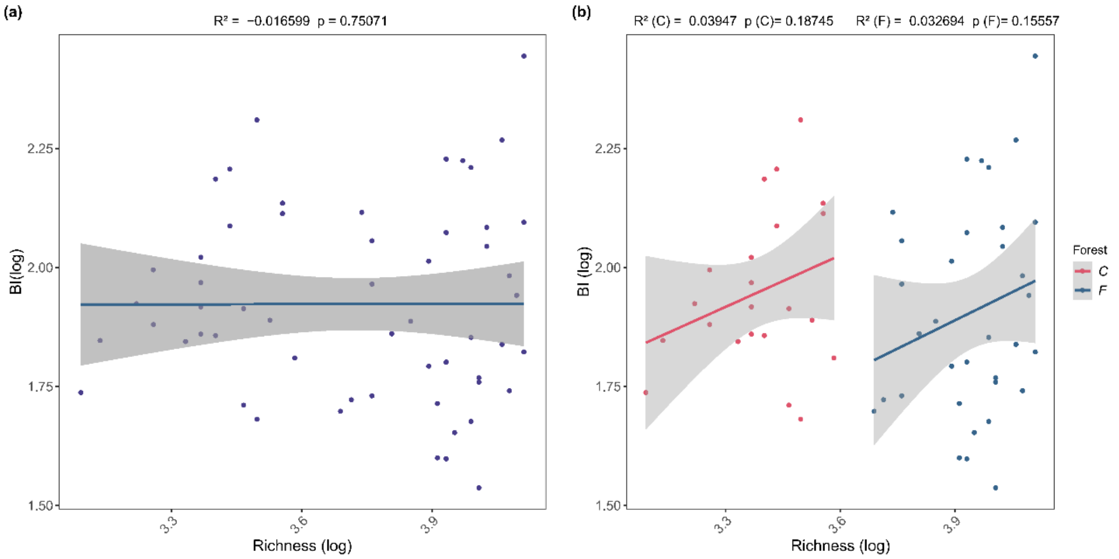


Figure S5. Relationships of the acoustic indices with richness: Bioacoustic index (BI) in the Paraguayan Chaco. Relationship included the entire community (continuous forest and corridors) (a), corridors (red points) and continuous forest (blue points) (b). Shaded areas are 95% confidence intervals.



Conclusões Gerais

O presente trabalho visou caracterizar os efeitos das mudanças da estrutura da paisagem decorrentes da perda de hábitat e fragmentação na composição e diversidade da comunidade de aves do Chaco Seco Paraguaio, assim como suas potenciais implicações no microambiente e na utilização dos índices acústicos como ferramenta de avaliação rápida das comunidades de aves, visando aumentar os estudos em áreas ameaçadas como o Chaco Seco. Esse estudo foi conduzido no Chaco Paraguaio, reunindo um conjunto de dados primários de comunidade de aves e coletados em campo na área de estudo durante a estação seca, visando contribuir com a conservação de uma das regiões menos estudadas do Gran Chaco, altamente ameaçada e desaparecendo rapidamente. Como fechamento da tese destacamos as conclusões gerais do trabalho:

1. As mudanças de cobertura da terra no Chaco Paraguaio têm levado a uma perda de hábitat e fragmentação da paisagem, criando duas dinâmicas diferentes, de expansão agrícola e de ocupação da terra. Assim, a paisagem se caracteriza por florestas contínuas, fragmentos e por corredores florestais, estruturas com o potencial de conectar a paisagem.
2. A perda e fragmentação de hábitat afetaram as facetas da diversidade de aves de forma distinta, com a diversidade funcional e filogenética sendo mais fortemente afetadas pela fragmentação do que a diversidade taxonômica, desta forma, mudanças na biodiversidade poderão passar despercebidas quando não forem avaliadas múltiplas facetas da biodiversidade e quando só focarmos em toda a comunidade de espécies. Para toda a comunidade de aves, a quantidade de habitat e fragmentação explicaram a variação, e a diversidade aumentou com a maior complexidade da paisagem. Isso foi diferente para as aves florestais, onde a fragmentação florestal foi a variável mais importante explicando a variação na diversidade. A mudança da paisagem não leva necessariamente a uma perda geral na diversidade, mas desencadeia uma rotatividade na composição da comunidade, o que inclui aves generalistas que se beneficiam da heterogeneidade da paisagem e substituem outras espécies, sendo as aves florestais as mais afetadas pela fragmentação.
3. A resposta das aves foi diferente quando focava em toda a comunidade de aves *versus* analisar apenas a comunidade de aves da floresta, sendo estas últimas as mais ameaçadas pelo nível de dependência da floresta.

4. As comunidades de aves usam os corredores florestais, no entanto esse uso depende de fatores ambientais e da estrutura da vegetação associados aos remanescentes. As comunidades de aves respondem diferentemente ao microambiente, principalmente as aves especialistas, que são menos adaptadas aos ambientes abertos, menos tolerantes ao aumento da temperatura e dependentes da cobertura do dossel e à densidade do sub-bosque. Porém, altas temperaturas são críticas para a atividade das aves no Chaco Seco.
5. Os índices acústicos foram sensíveis à complexidade da paisagem, refletindo diferentes respostas nas riquezas de aves da floresta contínua e corredores florestais. Assim, a complexidade da floresta contínua não foi expressa nos índices acústicos. Da mesma forma, este estudo destaca a necessidade de usar índices acústicos como avaliação rápida, visando potencializar os estudos da biodiversidade em áreas ameaçadas como o Chaco Seco.
6. A heterogeneidade do hábitat decorrentes da perda e fragmentação do hábitat atuam em grande escala afetando a estrutura da paisagem e localmente influenciando no microambiente. A composição e diversidade da comunidade de aves responderam à heterogeneidade da paisagem, que influenciaram nas respostas dos índices acústicos e as mudanças no microambiente.
7. Por fim, este trabalho deixa um precedente dos efeitos da perda de hábitat e fragmentação nas comunidades de aves no Chaco Seco Paraguaio, contribuindo com a incipiente disciplina de paisagens acústicas, esperando aprimorar ações de conservação na paisagem, e principalmente no contexto do Gran Chaco e sua biodiversidade.