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Dimensões funcionais e geográficas no espaço funcional de Aves das savanas tropicais

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Dimensões funcionais e geográficas no espaço funcional de Aves das savanas tropicais

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

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Lais Alves Moreira Brasileiro

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We've got five years, stuck on my eyes

Five years, what a surprise

We've got five years, my brain hurts a lot

Five years, that's all we've got (David Bowie)

SUMÁRIO

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RESUMO

Savanas se estendem por cerca de 20% da superfície terrestre, o que faz desse bioma um componente essencial para a conservação da biodiversidade tropical. As aves estão amplamente presentes em todos os continentes, formando comunidades ricas em espécies adaptadas aos diferentes estratos da vegetação das savanas e interagindo em múltiplos níveis tróficos, desempenhando diversas funções ecológicas. No entanto, essa diversidade associada às savanas está ameaçada pelo ritmo acelerado de degradação do bioma. Devido a processos biogeográficos e evolutivos, as avifaunas das savanas tropicais na América do Sul, África e Austrália diferem significativamente em termos taxonômicos. Análises comparativas de diversidade baseadas apenas na dimensão taxonômica revelam parte das potenciais diferenças e semelhanças ecológicas entre as savanas tropicais. A diversidade funcional torna-se, assim, uma ferramenta útil em estudos comparativos de faunas continentais, pois as espécies compartilham características funcionais entre si. O conjunto de espécies de cada savana define as características estruturais da diversidade funcional; entretanto, padrões de degradação do bioma podem contribuir para uma erosão funcional mais ou menos acelerada. Isso implica em uma relação recíproca entre o espaço funcional e o espaço geográfico onde as espécies estão distribuídas. Dessa forma, o objetivo central desta pesquisa é avaliar de maneira sistemática a estrutura da diversidade funcional das aves nas savanas do Brasil, África Subsaariana e Austrália, por meio da construção do morfo espaço ocupado pelas espécies, além de investigar como padrões espaciais de conversão de áreas naturais ameaçam essa diversidade em suas dimensões funcionais e geográficas. A comparação pantropical entre estruturas funcionais identificou padrões únicos e vulnerabilidades dos conjuntos de espécies de aves nas savanas do Brasil, África Subsaariana e Austrália, revelando características essenciais para o desenvolvimento de planos de conservação adequados às especificidades ecológicas de cada região. No contexto do Cerrado, a pesquisa mapeia a diversidade funcional das aves em relação à perda de cobertura vegetal nativa. Observou-se que 41% das áreas de distribuição das espécies estão afetadas pela perda de habitat, gerando consequências funcionais variadas. Algumas regiões do Cerrado apresentam estruturas funcionais mais vulneráveis, destacando a necessidade de estratégias de conservação direcionadas para proteger funções ecológicas essenciais. Além disso, a distribuição espacial dos atributos funcionais não está completamente alinhada com a riqueza funcional, ressaltando a importância dos padrões de distribuição de espécies dentro dos espaços funcionais. A análise do mapeamento recíproco entre esses dois espaços revelou que apenas 32,2% do espectro funcional das aves do Cerrado está ocupado, com regiões funcionais exibindo assinaturas geográficas distintas. A análise mostrou que muitas dessas regiões funcionais sofrem altos níveis de perda de vegetação, indicando que as ameaças espaciais possuem padrões de distribuição diferenciados dentro do espectro funcional, o que implica em consequências funcionais mensuráveis. O estudo identificou as células funcionais mais impactadas pela perda de habitat e mapeou as regiões onde ações de conservação são urgentemente necessárias para prevenir processos de erosão funcional na diversidade de aves do Cerrado. Em suma, a pesquisa demonstra o valor da diversidade funcional como ferramenta para o planejamento de conservação espacial e a importância de integrar conhecimentos baseados em características funcionais em estratégias de conservação para abordar a crise de perda de biodiversidade, especialmente em biomas subvalorizados como as savanas.

Palavra-chaves: Savanas; Aves; Diversidade funcional; Planejamento sistemático para conservação; Perda de habitat.

ABSTRACT

Savannas cover about 20% of the Earth's surface, making this biome an essential component for the conservation of tropical biodiversity. Birds are widely present across all continents, forming species-rich communities adapted to different strata of savanna vegetation and interacting across multiple trophic levels, performing various ecological functions. However, this diversity associated with savannas is threatened by the rapid rate of biome degradation. Due to biogeographical and evolutionary processes, the avifauna of tropical savannas in South America, Africa, and Australia differ significantly in taxonomic terms. Comparative diversity analyses based solely on the taxonomic dimension reveal only part of the potential ecological differences and similarities among tropical savannas. Functional diversity thus becomes a useful tool in comparative studies of continental faunas, as species share functional characteristics among themselves. The set of species in each savanna defines the structural characteristics of functional diversity; however, patterns of biome degradation can contribute to more or less accelerated functional erosion. This implies a reciprocal relationship between the functional space and the geographical space where species are distributed. Therefore, the central objective of this research is to systematically evaluate the structure of the functional diversity of birds in the savannas of Brazil, sub-Saharan Africa, and Australia, through the construction of the morphospace occupied by species, and to investigate how spatial patterns of natural area conversion threaten this diversity in its functional and geographical dimensions. The pantropical comparison between functional structures identified unique patterns and vulnerabilities in the bird species assemblages of the savannas of Brazil, sub-Saharan Africa, and Australia, revealing essential characteristics for developing conservation plans tailored to the ecological specificities of each region. In the context of the Cerrado, the research maps the functional diversity of birds concerning the loss of native vegetation cover. It was observed that 41% of the species' distribution areas are affected by habitat loss, generating various functional consequences. Some regions of the Cerrado exhibit more vulnerable functional structures, highlighting the need for targeted conservation strategies to protect essential ecological functions. Furthermore, the spatial distribution of functional traits does not fully align with functional richness, underscoring the importance of species distribution patterns within functional spaces. The analysis of the reciprocal mapping between these two spaces revealed that only 32.2% of the functional spectrum of Cerrado birds is occupied, with functional regions displaying distinct geographical signatures. The analysis showed that many of these functional regions experience high levels of vegetation loss, indicating that spatial threats have differentiated distribution patterns within the functional spectrum, leading to measurable functional consequences. The study identified the functional cells most impacted by habitat loss and mapped regions where conservation actions are urgently needed to prevent functional erosion processes in the bird diversity of the Cerrado. In summary, this research demonstrates the value of functional diversity as a tool for spatial conservation planning and the importance of integrating knowledge based on functional traits into conservation strategies to address the biodiversity loss crisis, especially in undervalued biomes such as savannas.

Key-words: Savanas; Aves; Functional diversity; Systematic conservation planning; Habitat loss.

APRESENTAÇÃO GERAL

A presente tese tem como objetivo aprofundar a compreensão sobre as consequências funcionais da crise de perda de biodiversidade, um campo de crescente interesse devido à sua importância para a manutenção do funcionamento de sistemas ecológicos dos quais a civilização humana depende (IPBES, 2019). Através dos processos de mudança no uso da terra, a perda de habitat tem sido apontada como um dos principais fatores da perda de biodiversidade em todo o mundo (Foley et al., 2005; Newbold et al., 2015). Consequentemente, o ser humano e sua chamada "civilização" são protagonistas nessa perda da diversidade biológica do planeta. A pegada ecológica humana é de tal magnitude que paisagens biológica e ecologicamente intactas, livres de distúrbios antropogênicos, representam apenas 23% da superfície terrestre do planeta (Watson et al., 2016). Cerca de 40–50% das áreas ocupadas foram convertidas em paisagens quase homogêneas, dominadas por áreas urbanas ou agrícolas (Chapin, Zavaleta et al., 2000; Barnosky et al., 2012). Essas paisagens simplificadas abrigam comunidades menos diversas do que aquelas originalmente presentes nos sistemas nativos (Tscharntke et al., 2005; Schipper et al., 2008; Flynn et al., 2009). Consequentemente, as intervenções humanas indiscriminadas interferem tanto na estrutura quanto no funcionamento dos ecossistemas (Hooper et al., 2012), muitas vezes resultando em sistemas menos adaptáveis e altamente vulneráveis a distúrbios e condições ambientais em mudança (Folke et al., 2002).

As áreas nativas do planeta não são exploradas e consideradas para proteção de maneiras iguais pelo homem. Savanas e outras áreas de vegetação aberta, por exemplo, representam biomas que cobrem cerca de 20% da superfície da terra (Pennington et al. 2018), mas não recebem a mesma importância que florestas úmidas no quesito de esforços de conservação. No Brasil, biomas como o Cerrado, são conhecidos como "biomas de sacrifício" devido a evidente destinação de suas áreas naturais para produção agrícola. Há uma discrepância significativa entre as áreas protegidas estabelecidas em biomas florestais e não florestais na faixa tropical (Murphy et al., 2016). Isso faz com que savanas e outras formações abertas sejam reconhecidas como biomas em risco devido aos altos níveis de pressão enfrentados por seus remanescentes e aos baixos níveis de proteção (Hoekstra et al., 2005; Overbeck et al., 2015; Pennington et al., 2018; Buchadas et al., 2022). Todo esse cenário vem com um custo altíssimo e pressão sobre a biodiversidade desse bioma tropical, com consequências ecológicas e funcionais ainda desconhecidas.

Savanas tropicais representam uma diversidade de perfis e paisagens de origens e histórias biogeográficas diferentes. Isto é, esse bioma tropical é composto por diferentes representantes, cada qual com suas particularidades taxonômicas, funcionais, contextos ecológicos e estados de conservação (Solbrig, 1996; Ratnam et al., 2011; Buchadas et al. 2022). Um grupo bastante presente nesses biomas são as Aves (Franchin et al. 2008). As Aves formam comunidades ricas em espécies, adaptadas aos diferentes estratos da vegetação, estabelecendo interações em múltiplos níveis tróficos e desempenhando papéis ecológicos importantes como polinizadores, dispersores de sementes e predadores (Barnagaud et al., 2019; Tobias et al., 2020). O aspecto da biodiversidade associado aos papéis ecológicos das espécies é conhecido como diversidade funcional, e seu estudo destaca que a crise global de perda de espécies tem consequências além da dimensão taxonômica. Em outras palavras, a perda de espécies em resposta a pressões globais como a perda de habitat resulta na perda de estratégias ecológicas associadas à manutenção das funções dos ecossistemas (Cooke et al., 2019).

Nos últimos anos, a pesquisa sobre a diversidade funcional e as consequências da perda de espécies tem avançado significativamente, evidenciando os possíveis caminhos de erosão funcional que os sistemas terrestres podem enfrentar nos próximos anos (Cooke et al. 2019; Carmona et al. 2021; Toussaint et al. 2021). No entanto, ainda existem lacunas, especialmente no que diz respeito à aplicação desses conhecimentos para informar ações de planejamento sistemático voltadas para a conservação. Diante disso, esta tese visa contribuir para o corpo de estudos que busca destacar a importância da dimensão funcional da biodiversidade, oferecendo novas perspectivas e abordagens para sua conservação.

Considerando a importância ecológica das aves e o papel crucial para a conservação da biodiversidade das savanas tropicais, utilizaremos as aves de savanas como objeto de estudo, com o objetivo geral de compreender como a diversidade funcional das aves de savanas tropicais está estruturada, quais são suas características, vulnerabilidade e como os padrões de destruição de savanas ameaçam essa dimensão da biodiversidade e suas funções e serviços ecossistêmicos associados. Para alcançar o objetivo proposto a tese foi dividida em três capítulos.

O primeiro capítulo da tese, mediante uma comparação sistemática das estruturas funcionais emergentes do conjunto de espécies de aves presentes em três grandes savanas do Brasil, África sub-saariana e Austrália, tem como objetivo identificar padrões únicos e compartilhados da diversidade funcional de aves de savanas tropicais que possam direcionar estratégias de conservação comuns ou específicas aos contextos ecológicos de cada região. Este capítulo foca em descrever com detalhes os espaços funcionais e suas propriedades, fornecendo uma base sólida para a compreensão dos conceitos explorados nos capítulos seguintes.

O segundo capítulo direciona sua investigação ao bioma neotropical savânico do Cerrado, buscando explorar a variação espacial de atributos chave da diversidade funcional e suas interações com os padrões de destruição das áreas nativas do bioma. O objetivo aqui é mapear os possíveis impactos funcionais da perda de hábitat no Cerrado, identificar vulnerabilidades funcionais e propor direcionamentos para ações de conservação com diferentes propósitos. Esse segundo capítulo oferece reflexões sobre o significado ecológico das estruturas funcionais e suas implicações para conservação, apresentando uma abordagem prática para incorporação do racional e das ferramentas analíticas de diversidade funcional em trabalhos de planejamento espacial para conservação, uma ideia que será aprofundada no terceiro capítulo da tese.

Por fim, o terceiro capítulo busca avançar na conservação de estruturas funcionais através da aplicação do conceito da Dualidade de Hutchinson para propor uma abordagem de conservação da diversidade funcional baseada na existência de uma relação recíproca entre espaço geográfico e espaço funcional. Este capítulo busca incorporar as contribuições anteriores da tese em uma abordagem nova de planejamento espacial voltado para a conservação da diversidade funcional.

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Capítulo 1

Pinpointing differences for conservation: an intercontinental comparison of the functional structure of bird diversity in tropical savannas

INTRODUCTION

In general, savannas can be defined as regions of natural vegetation characterized by a vegetative structure composed of discontinuous areas of tree cover and continuous areas of open vegetation (Scholes & Archer, 1997; House et al., 2003). Within this concept, there is a diversity of landscapes that vary in the proportions and compositions of their woody systems. (Ratnam et al., 2011). Thus, when we think of savannas, we can envision many profiles, highlighting its complexity and the challenges of a single definition for this important biome. This landscape diversity reflects the biome's geographical magnitude. The distribution of savannas encompasses large regions of South America, Africa, Asia, and Australia, covering approximately 20% of the global surface (Pennington et al., 2018). Savannas cover approximately 45% of sub-Saharan Africa and over 2 million km² in northern Australia (Woinarski et al., 2020), making this biome crucial for safeguarding biodiversity in the Tropics. In high diversity countries like Brazil, non-forest ecosystems represent one third of its territory (Ernst et al., 2022), with the Cerrado, an important center of endemism and the most biodiverse tropical savanna in the world (Myers et al., 2000; Colli et al., 2020), being the second largest biome, only behind the great Amazon Rainforest.

Unfortunately, the geographical magnitude and conservation importance of the savanna biome is not reflected in the efforts allocated to its protection. There is a significant discrepancy between protected areas established in forest and non-forest biomes in the tropical belt (Murphy et al., 2016). This imbalance originates primarily due to the Neotropical region, where forests such as the Amazon have up to 50% of their extent under some degree of protection, while this figure for its non-forest neighbor, the Cerrado, does not reach 10%. Savannas and other open formations are recognized as biomes at risk due to the high levels of pressure faced by their remnants and low levels of protection (Hoekstra et al., 2005; Overbeck et al., 2015; Pennington et al., 2018; Buchadas et al., 2022). It is speculated that this forest bias in conservation originates from a misguided historical conception of savannas as successional stages or as derived environments, forged by human intervention (i.e., savannas as degraded forests. Bond & Parr, 2010; Aleman et al., 2018). As a consequence, savannas are marginalized relative to forests, despite the evolutionary particularities of these biomes and their importance for maintaining biodiversity and ecosystem functions globally (Parr et al., 2014; Veldman et al., 2015; Silveira et al., 2020; Bardgett et al., 2021).

Treating savannas as forests or neglecting their protection in favor of forests comes at a high cost to the rich biodiversity sustained by this biome (Braithwaite, 1990; Myers et al., 2000; Murphy et al., 2016). Savannas are multiple, and not even the widely adopted structural definition is capable of capturing the functional particularities of its representatives (Ratnam et al., 2011). A particularly important group to be studied for their diversity in tropical savannas are birds. Birds are substantially present on all continents and oceans, forming species-rich communities adapted to the different strata of savanna vegetation, where they establish interactions with multiple trophic levels.

Due to biogeographical and evolutionary processes, the avifaunas of tropical savannas in South America, Africa, and Australia differ substantially in taxonomic terms (Franchin, 2018). However, these savannas also differ in terms of geographical extent, diversity of ecoregions, types of dominant vegetation, degree of influence from neighboring biomes, and time of isolation to name a few (Braithwaite, 1990; Solbrig, 1996; Dinnerstein et al., 2017). Ultimately, these aspects influence the composition and the number of species present in a region, meaning that comparative analyses of diversity focused solely on the taxonomic dimension elucidate only part of the potential differences and similarities between tropical savannas.

As a step further, functional diversity can be a tool used to describe continental faunas in comparative studies because species share functional characteristics among themselves. Functional diversity is a component of biodiversity, and its study focuses on analyzing communities based on the roles played by organisms (Petchy & Gaston, 2006). The unit of measurement shifts from species to functional traits that can be described as morphological, physiological, phenological, or behavioral characteristics that govern the functional roles or fitness of organisms in the environments they occupy (Violle et al., 2007). Thus, the definition of the "functional" aspect of interest depends on the selected traits (Palacio et al., 2022), with some authors even refraining from using the term and replacing it with ‘trait diversity’ (Germain et al. 2023). However, in general, the different functional combinations manifested by species reflect the diversity of ecological strategies, or roles, present in communities (Cooke et al., 2019; Carmona et al., 2021). In birds, morphological traits are known to be associated with relevant ecological aspects of their species (e.g., behavior, diet, trophic niche, dispersal, and locomotion), so for this group, trait diversity can be translated to functional diversity with relative confidence (Pigot et al., 2020). Furthermore, species traits can be represented using standardized and continuous measures, enabling a more detailed and objective quantification of functional diversity and the emergent functional structure of communities (Tobias et al., 2022).

This study aims to systematically assess the functional diversity of bird species in the tropical savanna biomes of Brazil, sub-Saharan Africa, and Australia by constructing and comparing the morphospace occupied by the species assemblages of each savanna. Each morphospace represents the functional structure defined by the functional diversity within the savanna. This systematic approach has the potential to reveal unique patterns, similarities, and vulnerabilities of bird assemblages that extend beyond their taxonomic dimension. Comparative studies of the functional structures of continental faunas are crucial for developing comprehensive conservation plans for savanna biodiversity and for identifying appropriate strategies tailored to the ecological context of each savanna, thereby supporting the conservation of the functional backbone underlying a biome's functioning (Corlett & Primack, 2006).

Thus, the goal of this study is to conduct an intercontinental comparison of the functional structure emerging from the bird diversity present in three major tropical savannas located in South America, sub-Saharan Africa, and Australia. As general patterns, we expect that the African savanna, due to its largest geographical extent and the highest number of species, should harbor the greatest functional richness among the regions. Meanwhile, for the Australian savanna, owing to its longer evolutionary isolation, we expect it to exhibit the most functionally differentiated fauna among the three studied savannas. Because of a global pattern of concentration of the vast majority of bird species in a single neighborhood in previously mapped functional spaces (Pigot et al., 2020; Carmona et al. 2021; Toussaint et al. 2021), we expect that the functional structures of continental bird faunas should not differ significantly from this global pattern. However, due to the ecologically structured way bird diversity is organized (Pigot et al. 2020; Tobias et al. 2020), we expect to observe more defined differences between continental faunas on a more ecologically defined scale, such as of trophic niche.

METHODS

Study area

The study area encompasses large savanna regions located in Brazil, tropical Africa, and Australia (Figure 1). This geographical delineation represents the primary biogeographic savanna regions in the tropics, incorporating structurally similar regions but with distinct natural histories (Archibald et al., 2020). Specifically, the savanna boundaries used in this study include all ecoregions classified under the "Tropical & Subtropical Grasslands, Savannas & Shrublands" category by Dinerstein et al. (2017). The "Flooded Grasslands & Savannas" and "Desert & Xeric Shrublands" classes were not included in the study. Ecoregion data were obtained from Dinerstein et al. (2017).

Figure 1. Study Area Representation. The color-blocked regions depict biome categories as classified by Dinerstein et al. (2017). Orange-shaded areas indicate the extent of Tropical and Subtropical Grasslands, Savannas & Shrublands. Our study focuses on specific regions within this category: the Brazilian Cerrado (highlighted in the central orange portion of South

America), sub-Saharan Africa, and northern Australia. Data and visual representation retrieved from Dinerstein et al. (2017) and can be accessed at: https://ecoregions.appspot.com/

List of species

The species lists for each studied tropical savanna region were compiled in two steps. First, an advanced search was conducted on the IUCN website (https://www.iucnredlist.org/) to filter the global list of extant bird species recorded in each continent/region studied (i.e., South America, sub-Saharan Africa, and Oceania). For each species included in the study, the geographic distribution file was downloaded. The distribution maps are sourced from BirdLife International (http://www.birdlife.org/datazone/home) and represent the breeding distribution area of species. From this initial list, the limits of our studied savanna regions were gridded at about 110-km resolution (i.e., approximately 1° resolution) and we spatially filtered species falling within each savanna's grid. This resolution has been suggested as the most appropriate working on data of geographic distributions, as it reduces the inclusion of false presences at large spatial scales (Hurlbert and Jetz, 2011). Thus, our final species list represents those with distributions overlapping each studied savanna.

Measures of taxonomic diversity

Taxonomic diversity will be quantified in terms of species richness in the savanna region. Species richness will be calculated as the total number of species whose distributional range falls within the savanna's boundaries.

Measures of functional diversity

Functional traits

In order to characterize the diversity of birds in each savanna in a comparable manner, functional data were collected for all listed species. The functional traits used here represent linear morphological measurements. Thus, the functional variation considered in this study directly relates to morphology. Linear measurements, although they do not geometrically capture the shape of species, have the advantage of being easily recorded. This allows for linear measurements of species from different sources to be gathered with less risk of error. All functional trait data were obtained from the AVONET database (Tobias et al., 2022).

The AVONET database (Tobias et al., 2022) represents a compilation of individual-level measurements for all extant bird species worldwide aggregated in a standardized manner at the species level. Among the information included in the database are nine linear morphological characters, including four bill measurements, three wing measurements, tarsus length, and tail length (Figure 2). The choice of morphological characters is based on their established associations with relevant ecological aspects of bird species such as diet, dispersal, and locomotion (Leisler & Winkler, 1985; Miles & Ricklefs, 1984; Pigot et al., 2020; Ricklefs & Travis, 1980).

Considering the association between morphology and ecology in birds, bird diversity will also be assessed in ecological categories based on diet data (Wilman et al., 2014; Tobias & Pigot, 2019) through trophic niche classes. Thus, all subsequent analyses will be conducted at the scale of the regional species pool and at the scale of the regional species pool belonging to each of the following trophic niches: frugivores, granivores, nectarivores, invertivores, vertivores and aquatic predators (Pigot et al., 2020).

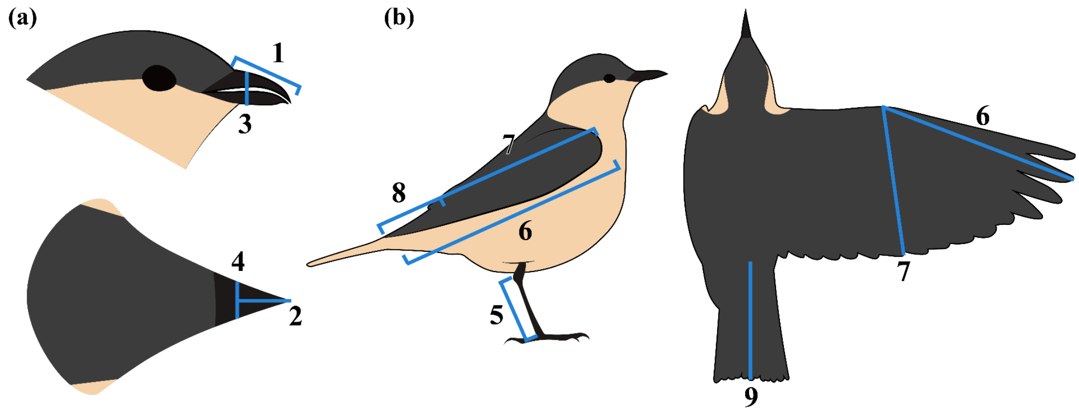

Figure 2. Illustration of the morphological characters compiled in the AVONET database (Tobias et al., 2022). a) Beak measures; b) Body measures. Figure is based on an original illustration by Richard Johnson published in Pigot et al. (2020), adapted by Isabella Silveira.

Functional structure

The ecomorphological data collected will serve as the basis for representing the functional structure of bird diversity in the studied savannas. With the selection of continuous traits, we constructed a functional space where each dimension represents a trait. This resulted in a multidimensional space where species are distributed according to their morphological characteristics (Villéger et al., 2008).

Before constructing the functional space, all traits were transformed and scaled to a mean of zero and a standard deviation of one (Palacio et al., 2022). The multidimensional spaces were constructed using a Principal Component Analysis (PCA) of the Euclidean distances between species. The dimensionality of this space was identified through a Horn parallel analysis using the \`paran´ package (Dinno, 2018) and by a PCA significance testing using the \`PCATest´ package (Camargo, 2022). The result of these steps will represent a reduced functional space composed of the main axes representing the functional variation of the bird fauna of each studied savanna (Cooke et al., 2019).

Estimating the Trait Probabilities Density functions (TPDs)

TPDs are probability density functions that reflect the likelihood of observing species with specific functional traits within the defined functional space. Thus, a TPD allows the mapping of the functional space as a probabilistic surface that can be analyzed both for its boundaries (i.e., functional richness) and for its occupancy pattern (i.e., species density distribution) (Carmona et al., 2016). The TPDs were defined by functions from the `TPD´ (Carmona et al., 2019) and `ks´ (Duong, 2007) packages. For this analysis, the kernel of each species was represented by a multivariate normal distribution centered on the species' coordinates in the space defined by the PCA. An optimal bandwidth parameter was defined by an unconstrained selector, following Carmona et al. (2019). The combination of kernels of all species represent the assemblage's TPD function of the functional diversity present in each one of the studied tropical savannas.

With the TPDs estimated, their surfaces were then segmented by a regular D-dimensional grid. Thus, the continuous variation of probabilities will be categorized, and a TPD value will be calculated for each cell (Carmona et al., 2019). The TPD value in each cell represents the species density in that particular area of the functional space. That is, the number of functionally similar species. The number of grid cells will be defined *a priori* and will depend on the dimensionality of the space. Following Toussaint et al. (2021), two-dimensional spaces can be divided into 40.000 cells of 200 x 200 units of variation. Due to their probabilistic nature, the TPDs will be graphically represented by highlighting their contours containing 50% and 99% of the total probability functions.

Functional diversity indices

The following multidimensional indices of functional diversity were calculated: functional richness and functional redundancy (Carmona et al., 2019). Functional richness will be quantified as the volume of the TPD that encompasses all species present in the functional space, representing the amount of functional combinations present in the community (Cornwell et al., 2006; Villéger et al., 2008; Carmona et al., 2019). Functional redundancy will be represented as the number of functionally similar species and will be calculated as the mean number of species that share trait values weighted by the probability of each trait in the community (Carmona et al., 2016). This mathematical definition of redundancy has a residual relationship with species richness. To neutralize the effect of the number of species on the redundancy index value and allow comparisons between savannas, relative redundancy values will be calculated by dividing redundancy values by the total number of species minus 1 (FRedrel = Fref / S – 1, where S = number of species in the community. (See Carmona et al., (2019) for mathematical definition).

Functional diversity's measures will be calculated for the assemblage of all species and for the assemblage of each niche trophic niche class. The quantification of multidimensional indices of functional diversity will be carried out using the correspondent functions from the `TPD´ package (Carmona et al., 2019).

Functional structures comparison

The regional functional diversities will be compared to the global functional structure (i.e., functional structure of the species pool across the entire studied region) by identifying how much of the global functional space is occupied by each region (Frich% = FrichRegional / FrichGlobal). The regional structures will be compared to each other both visually and in terms of similarity through measures of overlap of functional spaces (Carmona et al., 2019; Mammola, 2019). Thus, we will identify how each regional diversity contributes to the global functional structure of birds in tropical savannas.

RESULTS

The global sample for this study (Supporting information table 1), encompassing species from all savannas considered, included 3,431 species: 1,803 from Africa, 1,104 from the Cerrado, and 524 from Australia. In total, 31 taxonomic orders and 169 families were represented. Africa included 27 orders and 101 families, the Cerrado 24 orders and 72 families, and Australia 19 orders and 81 families (Table 1). Overall, invertivores, frugivores, granivores, nectarivores, vertivores and aquatic predators were the specialized trophic niches more represented by species number in our study region. Following results will focus on these groups.

All reduced functional spaces (global and regional PCAs) reflected biologically significant variations (global PCA: $\psi = 52.04$; $\varphi = 0.68$, $p < 0.05$). The Horn parallel analysis identified the first two components (PC1 and PC2) as the dimensions significantly associated with systematic sources of variation in the multivariate trait data. The other components were discarded for subsequent analyses.

Considering the entire set of species from the studied tropical savannas (global PCA), the first two PCs explained 83.7% of the total variation (Figure 3A). PC1 (70.4% [CI (95%): 69.1-71.5]) can be interpreted as a size index, with higher PC1 values indicating larger linear measurements of each considered trait. Meanwhile, PC2 (13.2% [CI (95%): 12.4-14.1]) has its variation associated with the traits of Kipp's Distance and Hand-Wing Index, indicating PC2 as a dimension representative of flight and dispersion capacities of bird species (Sheard et al., 2020).

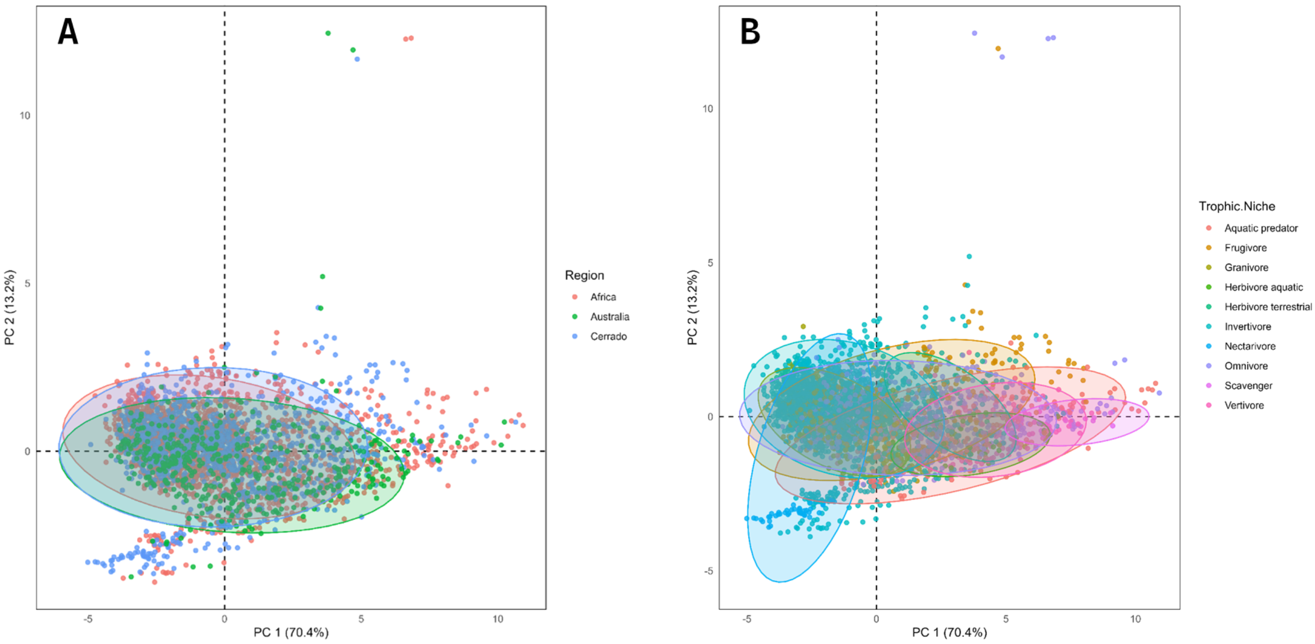

Figure 3. Visualization of the PCA summarizing the functional distribution of birds from the studied savannas. A) PCA conducted using the entire dataset. Each point represents a species and is color-coded to highlight their geographical location (Salmon – Africa, Green – Australia, and Blue – Brazil). B) Same PCA but points are color-coded to highlight the ecological groups of trophic niche in the global functional space. All ellipses represent 95% of the data.

The results observed in the global PCA are consistent across regions, except for the PC2 of the Cerrado region, that includes the additional influence of tarsus length, thereby incorporating another movement-related trait into this functional dimension associated with bird movement.

As expected, a high level of overlap is observed in the defined global functional space (Figure 3A, >97% shared space). This indicates that all regional faunas of the studied tropical savannas are predominantly concentrated in a similar portion of the functional space. When examining the arrangement of species at the ecological scale of the trophic niche, a more distinct functional compartmentalization of species within this highly overlapping space is observed (Figure 3B).

Considering all species, the functional diversity values within each studied savanna revealed the expected general pattern of correlation with taxonomic richness (Table 1). That is, in the tropical savannas studied, higher species richness accompanied greater functional richness and redundancy. As expected, Africa is the savanna region with the highest values of functional richness for birds, closely followed by the Cerrado and then Australia (Table 1, AlphaAfr = 92.36; AlphaCerr = 91.7; AlphaAus = 74.33). The proximity between the functional richness of Africa and the Cerrado is relevant as it reflects a high level of functional diversity contained within the smaller bird assemblage of the Cerrado. The Brazilian savanna contains 32.7% of the analyzed species pool, and within this parcel, holds up to 85.1% of the global functional space. This proportion of occupied space is equivalent to Africa's, which holds 53.3% of the species included in this study and occupies 85.7% of the global functional space (Figure 4). Lastly, Australia, as the least taxonomically diverse savanna region, contains 15.5% of the studied species. However, this smaller regional taxonomic diversity occupies up to 69% of the global functional space (Figure 4).

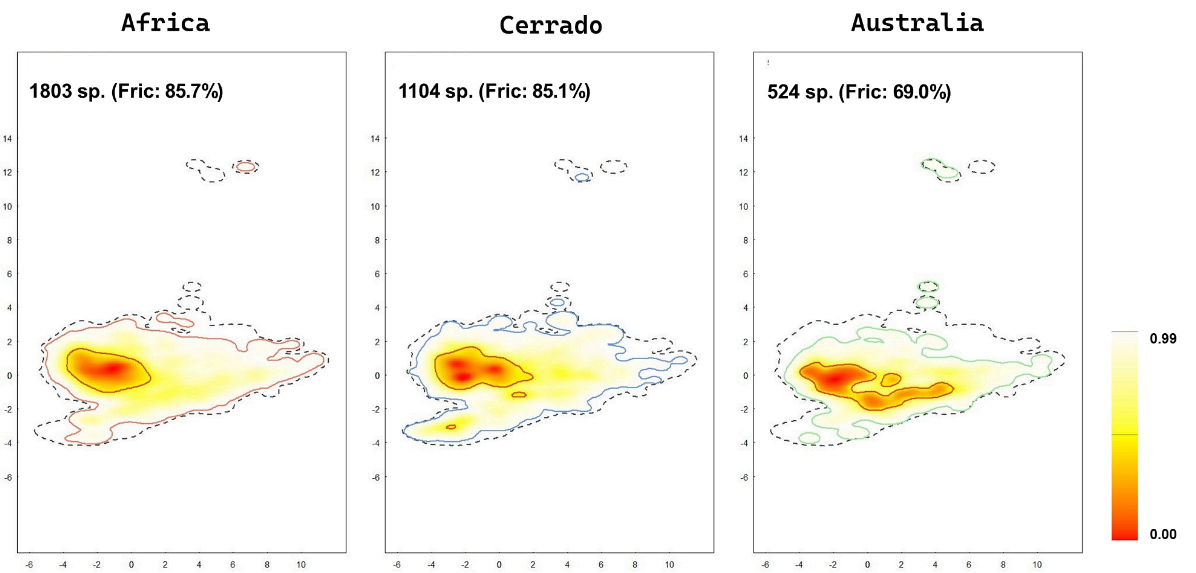

Figure 4. Functional structure depicted ad trait probability density functions (TPDs) of the studied bird faunas from tropical savanna regions located in Africa, Cerrado, and Australia. Each surface represents the probability distribution of species in the defined functional space. The yellow to red gradient represents species quantiles (i.e., the darker the

shade, the higher the species density). The black dashed line represents the 99% limits of the global space of the studied savannas. The inner bold red colored lines highlight the hotspots of each region (i.e., area occupied by 50% of the species). The inner colored lines represent the 99% limits of the functional space occupied by the regional faunas. TPDs are based on the PCAs used to ordinate the trait data, and the X and Y axis represent PC1 and PC2, respectively. In the upper left corner are the values of taxonomic richness and the proportion (%) of each regional functional diversity relative to the global.

Considering the regional species assemblages within each trophic niche, the functional diversity values in the studied savannas deviated from the expected correlation with taxonomic richness (Table 1). In the nectarivore group, the Cerrado had the highest taxonomic richness and functional redundancy, but Australia exhibited the greatest functional richness. This suggests that nectarivorous species in the Cerrado, despite being numerous, are morphologically similar and occupy a relatively small portion of the shared functional space (Figure 5). For frugivores, Africa had the highest functional redundancy, while the Cerrado showed the greatest taxonomic and functional richness. This indicates a somewhat packed distribution of most frugivorous species in the functional space defined by the African savannas (Figure 5). Among granivores, Africa led in taxonomic richness, functional richness, and redundancy, yet the Cerrado displayed the highest redundancy when this metric was adjusted for the total number of species. This pattern was also observed in the invertivore group, indicating that these comparatively smaller assemblages of the Cerrado exhibited more functional redundancy. For vertivores and aquatic predators, Australia's assemblages demonstrated the highest functional redundancy despite having the less numerous assemblages, both taxonomically and functionally, suggestive of species concentration to similar regions of the functional spectrum (Figure 5).

The distribution of species density across the described functional space provides insights into the functional redundancy of the regional assemblage. Depending on the number of functionally similar species, areas within the functional space (i.e., portions with specific combinations of morphological traits or ecological strategies) may be more or less vulnerable to potential species losses. In the case of the studied tropical savanna regions and considering all species, Africa emerged as the region with the highest redundancy, followed by the Cerrado and Australia (Table 1. Fred: [31.4 – 123.6]). When controlling for the number of species (i.e. relative redundancy), this gradient remained consistent, but now in much more similar proportions (Table 1. FRelRed: [0.060 – 0.069]), indicating that regional faunas exhibit comparable levels of functional redundancy for their respective number of species.

In terms of relative redundancy, we observe a different scenario for ecological groups. The African fauna, even in its comparatively more species-rich groups (e.g., granivores, invertivores, vertivores, and aquatic predators), reached intermediate redundancy values (Table 1). Thus, the Cerrado and Australian savannas stand out in terms of functional redundancy with comparatively higher values, even in groups where they do not excel in taxonomic and functional richness (Table 1). This indicates a higher functional dispersion of african species in the functional space.

Table 1. Diversity indices of the all species and ecological groups of each savanna region. Functional richness values were calculated based on the space occupied in the TPDs (Carmona et al., 2019). The highest values of each index are shown in bold. Only the most representative specialized trophic niches in terms of species number were illustrated.

Trophic Niche	Region	Taxonomic Richness	Functional Richness	Redundancy	Relative redundancy
All species	Africa	**1803**	**92.36**	**123.65**	**0.069**
	Cerrado	1104	91.7	69.753	0.063
	Australia	524	74.33	31.399	0.060
Nectarivores	Africa	37	9.3	15.472	0.430
	Cerrado	**48**	9.13	**21.645**	**0.461**
	Australia	20	**13.81**	4.425	0.233
Frugivores	Africa	132	35.36	**15.156**	**0.116**
	Cerrado	**135**	**46.6**	10.596	0.079
	Australia	21	19.85	1.712	0.086
Granivores	Africa	**217**	**28.71**	**35.557**	0.165
	Cerrado	51	21.70	10.899	**0.218**
	Australia	47	22.05	6.197	0.135
Invertivores	Africa	**926**	**73.32**	**76.394**	0.083
	Cerrado	588	64.77	59.046	**0.101**
	Australia	201	52.81	18.147	0.091
Vertivores	Africa	**76**	**26.08**	**10.173**	0.136
	Cerrado	47	22.02	5.858	0.128
	Australia	24	16.02	4.205	**0.183**
Aquatic predators	Africa	**116**	**50.4**	**6.560**	0.057
	Cerrado	69	44.84	3.669	0.054
	Australia	71	36.7	5.528	**0.079**

The redundancy values represent averages of functional neighborhoods (Carmona et al., 2016). Beyond its numerical measure, another important aspect to consider is the distribution of this redundancy or the pattern of occupation of species and ecological groups across the functional space. We observed that some ecological groups occupy more central positions of the occupied space (Figure 5. nectarivores, frugivores, and invertivores from Africa; granivores and invertivores from the Cerrado; nectarivores, granivores, and invertivores from Australia), while others occupy more peripheral positions (Figure 6. vertivores and aquatic predators from Africa; nectarivores, vertivores, and aquatic predators from the Cerrado; vertivores and aquatic predators from Australia). Due to the high overlap of species in the functional space, peripheral groups have lower species density compared to central groups, representing less redundant functional combinations and defining the limits of the observed functional space. In contrast, central groups are mainly located near regional hotspots, representing more redundant functional combinations (Figure 5).

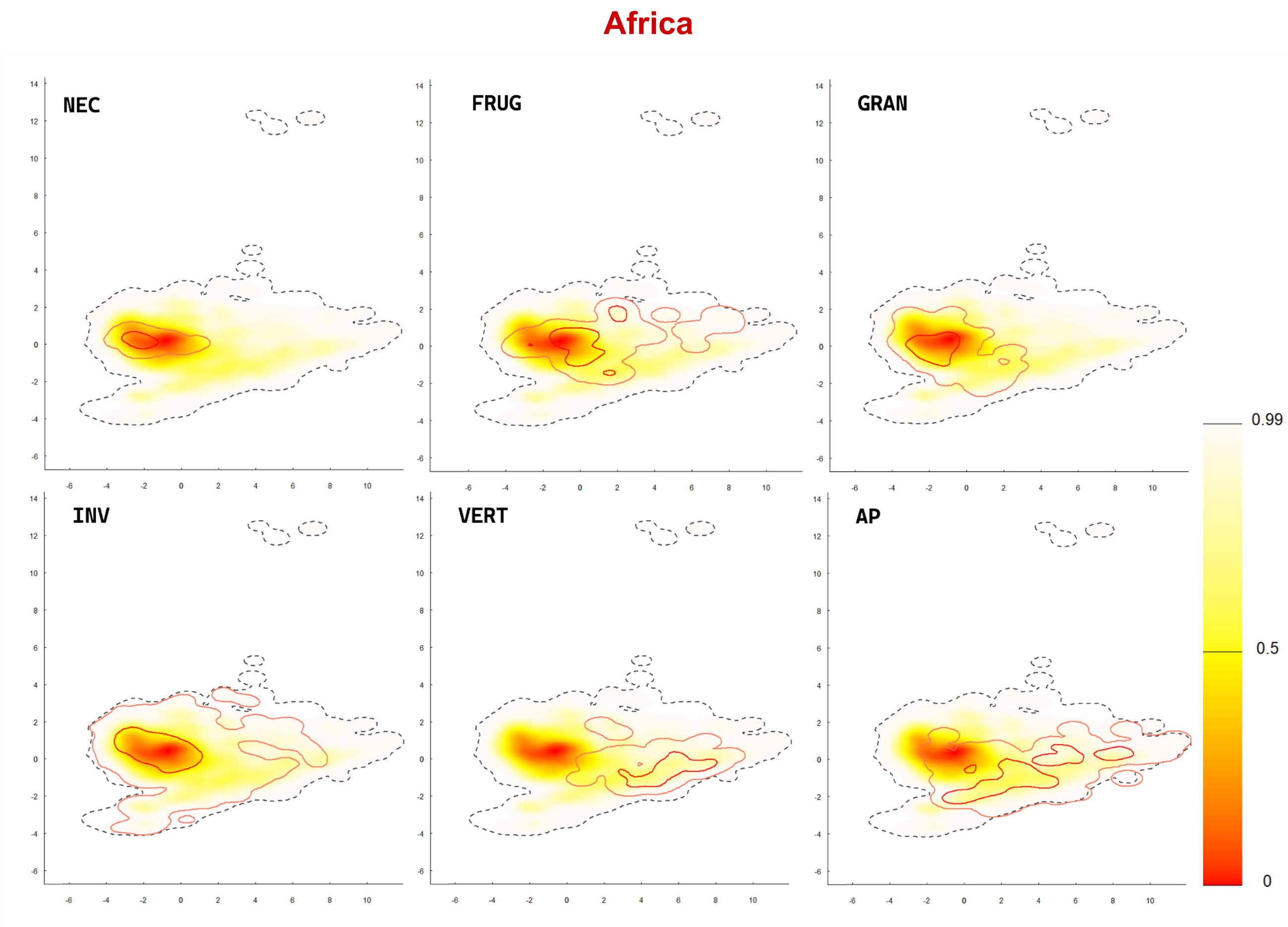

Figure 5. Functional structure depicted as trait probability density functions (TPDs) of the ecological groups of trophic niche of birds from each studied tropical. Each surface represents the probability distribution of species in the defined functional space. The yellow to red gradient represents the species quantile (i.e., the darker the shade, the higher the species density). Black dashed lines represent the 99% limits of the global space of the studied savannas. Light colored lines represent the 99% limits of the functional space occupied by each regional ecological group. Bold colored lines define the regional hotspots of each ecological group (i.e., area concentrating 50% of the species). Red = Africa, Blue = Cerrado, and Green = Australia).

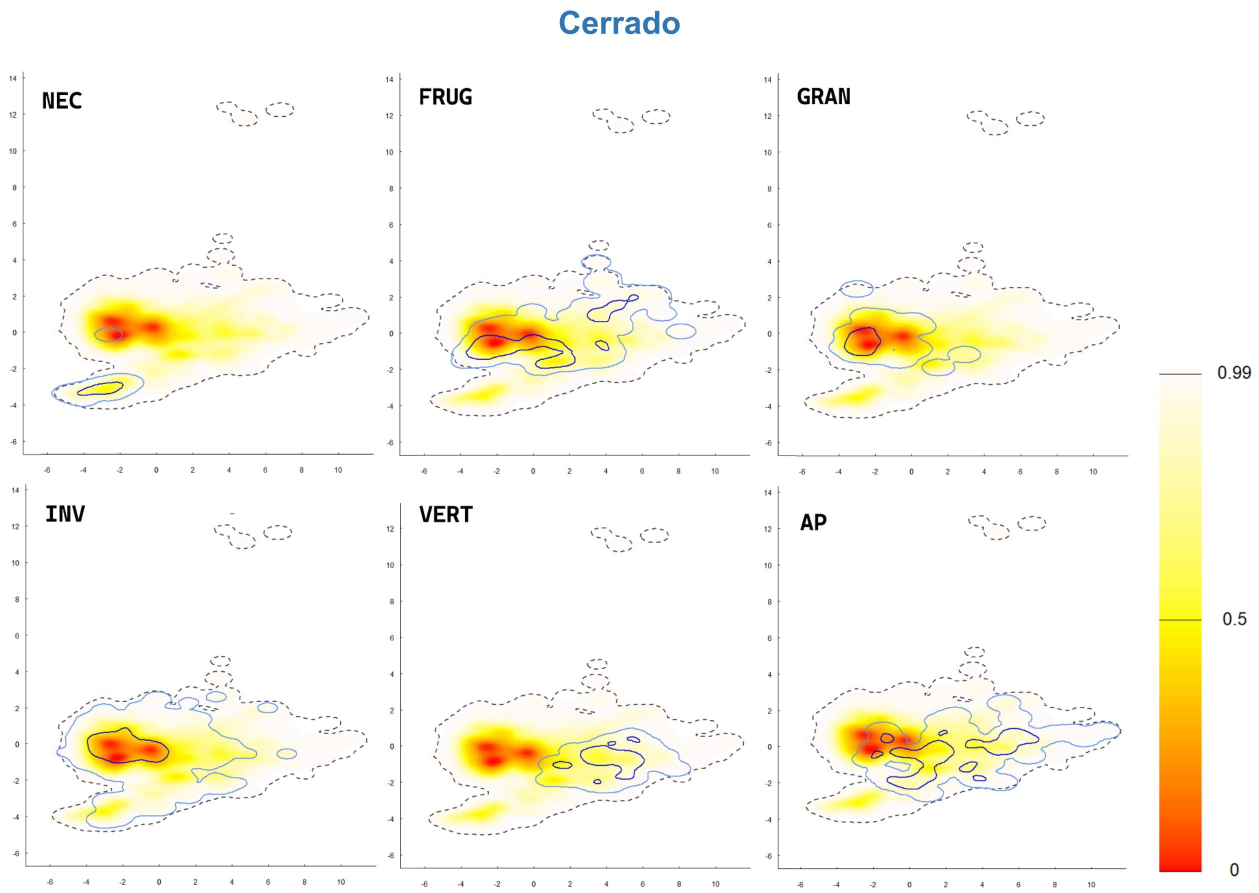

Figure 5. Functional structure depicted as trait probability density functions (TPDs) of the ecological groups of trophic niche of birds from each studied tropical. (Cont)

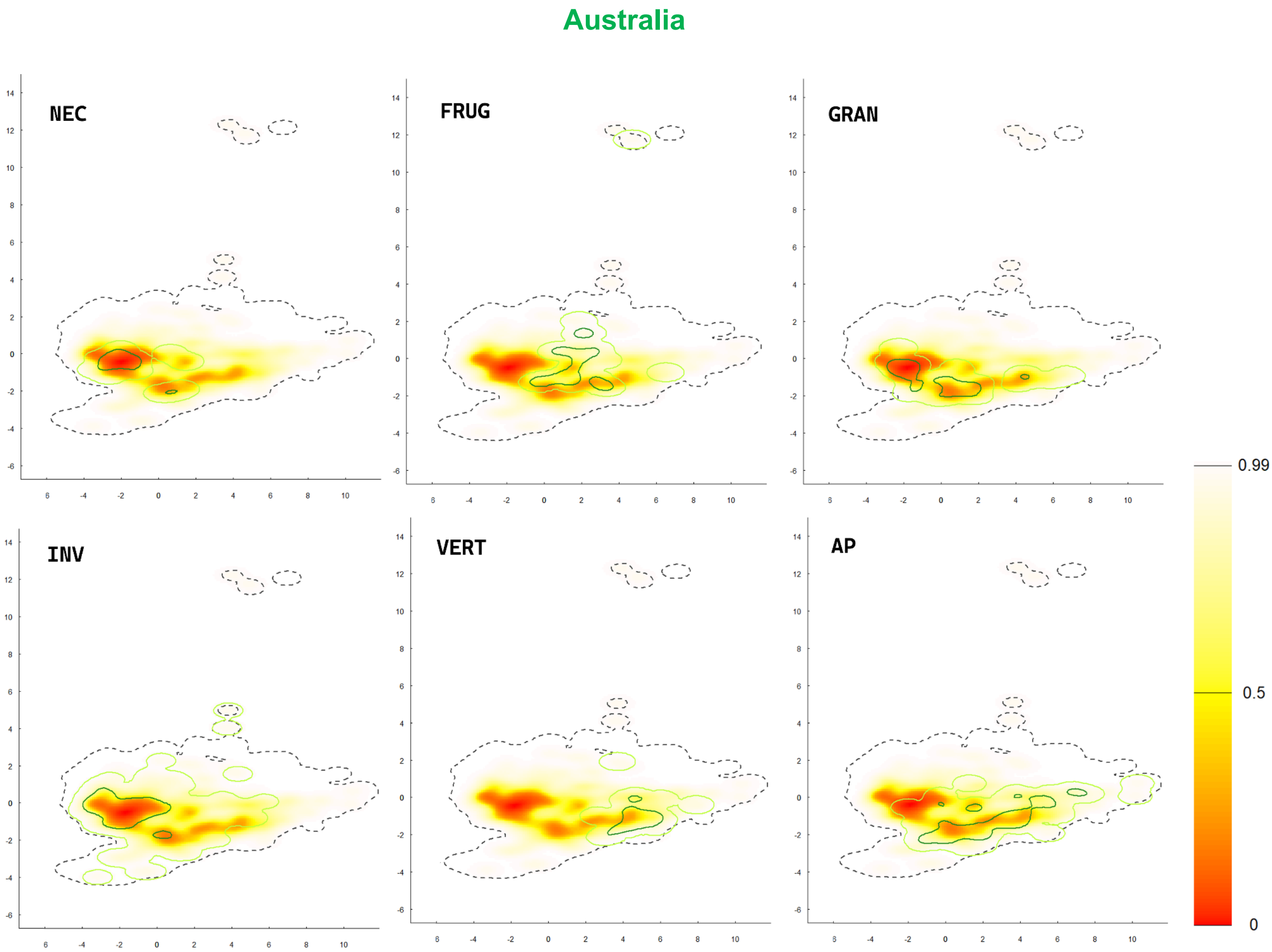

Figure 5. Functional structure depicted as trait probability density functions (TPDs) of the ecological groups of trophic niche of birds from each studied tropical. (Cont).

The observed differences in patterns of occupation of the functional space for each savanna reflect only moderate dissimilarity between savannas, but indicate Australia as the most dissimilar region (0 = Total similarity and 1 = Total dissimilarity: FDivBeta Cerrado-Australia: 0.340; FDivBeta Africa-Australia: 0.312; FDivBeta Africa-Cerrado: 0.177). As expected, more pronounced differences emerge at the ecological scale of trophic niches (Figure 6). On average, the dissimilarity among groups ranged from 0.60 to 0.92 (Table 2). These high values reflect the observed morphological signature of the trophic niches in the occupied functional space of each savanna (Figure 5). However, when comparing the same trophic niche across regions, we also observe significant separations (Table 3). This highlights the ecological and geographical factors in the evolution of these functional signatures. An extreme case is the almost unique functional structure formed by the nectarivorous birds of Cerrado (Figure 6. Fdissim Cer-Aus = 0.97; FDissim Cer-Af = 0.97; Mean FDissimAll = 0.92). This exclusive functional contribution of Cerrado is mainly defined by the Trochilidae family.

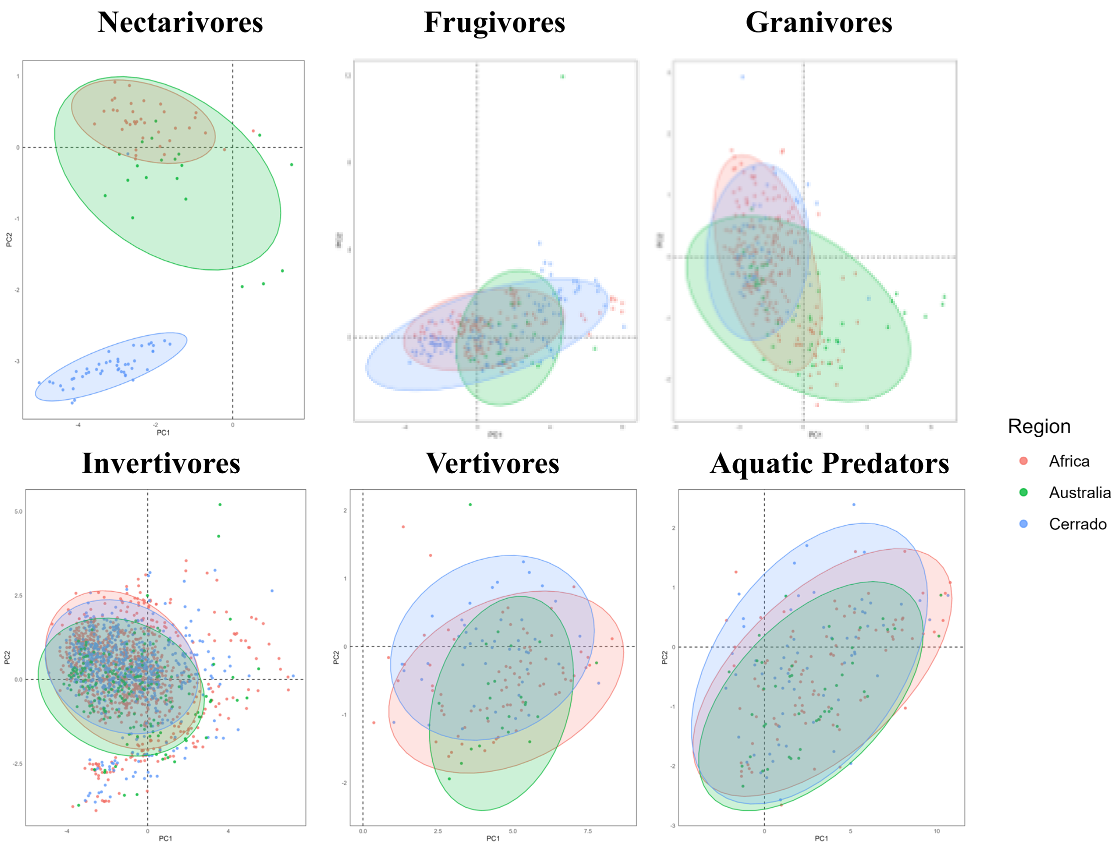

Figure 6. Functional separation of ecological niche groups in each studied tropical savanna region. Each plot represents an ecological group of trophic niche. Regions are highlighted by colored ellipses that capture 95% of their data in the functional space defined by the global PCA.

Table 2. Summary of functional dissimilarity values among all functional groups from all regions (FdissimAll). Mean, minimum, and maximum functional dissimilarity values are presented by group and by region. The regional group that forms the pair in the dissimilarity analysis is indicated in parentheses. The index ranges from 1 to 0, with 1 being total dissimilarity and 0 being total similarity. AF = Africa; AUS = Australia; CER = Cerrado; NEC = Nectarivores; FRUG = Frugivores; GRAN = Granivores; INV = Insectivores; VERT = Vertivores; AP = Aquatic predators.

Trophic Niche	**Region**	***Mean dissimilarity***	**Min dissimilarity**	**Max dissimilarity**
Nectarivores	Africa	0.774	0.503 (CER GRAN)	1.0 (AUS VERT)
	Cerrado	0.925	0.943 (AF INV)	1.0 (AF VERT, CER VERT, AUS FRUG, AUS VERT)
	Australia	0.689	0.436 (AF GRAN)	0.996 (AUS VERT)
Frugivores	Africa	0.677	0.504 (CER INV)	0.980 (CER NEC)
	Cerrado	0.633	0.473 (AUS INV)	0.979 (CER NEC)
	Australia	0.755	0.637 (AF FRUG)	1.0 (CER NEC)
Granivores	Africa	0.628	0.350 (AUS INV)	0.988 (AUS VERT)
	Cerrado	0.665	0.384 (AF GRAN)	0.979 (CER NEC)
	Australia	0.658	0.533 (AUS NEC)	0.979 (CER NEC)
Invertivores	Africa	0.621	0.208 (CER INV)	0.959 (AUS VERT)
	Cerrado	0.633	0.208 (AF INV)	0.973 (AUS VERT)
	Australia	0.600	0.333 (AF INV)	0.950 (CER NEC)
Vertivores	Africa	0.736	0.418 (CER VERT)	1.0 (CER NEC)
	Cerrado	0.745	0.418 (AF VERT)	1.0 (CER NEC)
	Australia	0.809	0.453 (AF VERT)	1.0 (AF NEC, CER NEC)
Aquatic predators	Africa	0.656	0.379 (CER AP)	0.989 (CER NEC)
	Cerrado	0.644	0.379 (AF AP)	0.992 (CER NEC)
	Australia	0.667	0.317 (AF AP)	0.987 (CER NEC)

Tabela 3. Functional dissimilarity within ecological groups. Values are presented for each ecological group of trophic niche and each region pair compared. Dissimilarity index varies between 1 and 0, indicating total dissimilarity and total similarity, respectively.

Trophic Niche	Region pair	Dissimilarity
Nectarivores	Africa - Cerrado	0.979
	Africa - Australia	0.654
	Cerrado - Australia	0.979
Frugivores	Africa - Cerrado	0.580
	Africa - Australia	0.637
	Cerrado - Australia	0.727
Granivores	Africa - Cerrado	0.384
	Africa - Australia	0.489
	Cerrado - Australia	0.601
Invertivores	Africa - Cerrado	0.208
	Africa - Australia	0.333
	Cerrado - Australia	0.372
Vertivores	Africa - Cerrado	0.418
	Africa - Australia	0.453
	Cerrado - Australia	0.566
Aquatic predators	Africa - Cerrado	0.379
	Africa - Australia	0.317
	Cerrado - Australia	0.441

DISCUSSION

We conducted a pantropical assessment of the functional diversity of the bird fauna in three major tropical savanna biomes in Brazil, sub-Saharan Africa, and Australia and compared the functional structures defining these diversities. Our analysis identified both shared and unique patterns among the bird faunas of each savanna, highlighting important considerations for the conservation of the functional foundations that support the biodiversity of these biomes. First, we found that the functional space defined by savanna bird species can be characterized by two dimensions representing the birds' overall size and their flight or movement capabilities. The global functional space showed a high degree of overlap, with most species concentrated within a similar region of the functional spectrum. This pattern of overlap in birds' global functional spaces has also been documented in other studies using different sets of traits (Cooke et al. 2019; Pigot et al. 2020; Carmona et al. 2021), suggesting a strong underlying signal in the functional organization of birds. Despite the extensive shared functional space, each savanna exhibited a unique functional footprint, which became even more pronounced when examined at the ecological scale of trophic niche, highlighting the distinct ecological context of each savanna and their regional contributions to the structuring of the tropical savanna bird's functional space.

When analyzing the functional spectrum composed by all species of each savanna, we observed an expected pattern of functional and taxonomic diversity. It means that in the tropical savannas studied, greater species richness accompanied larger values of functional richness and redundancy. Regarding functional richness, Africa, the more geographically extensive region, was the most species rich savanna, concentrating more than half of the species included in this study. Despite this substantial difference in taxonomic diversity, the amount of functional space occupied by each savanna was comparable. The Cerrado, our Neotropical representative, concentrated just over 30% of the species and occupied an equivalent space to Africa in the functional spectrum. Just as impressive, Australia taxonomically contributed to only 15.5% of species, but its functional contributions to the global space amounted to 69% of its area. Furthermore, regarding functional redundancy values, when controlling for the total number of species, the studied savannas showed comparable levels of redundancy, indicating that tropical savannas show are regions of high functional richness and redundancy for birds, a pattern previously registered for the Neotropics (Cooke et al. 2019a). These results suggest that taxonomic metrics of diversity for regional assessments do not fully capture the magnitude of the functional component of biodiversity, and can not be used as the only diversity consideration in regional conservation assessments (Devictor et al. 2010).

Regional functional structures, when analyzed at the ecological scale of trophic niches, exhibited more pronounced differences and deviations from the expected patterns. Each trophic niche presented a distinct functional footprint in each savanna, reflecting a strong connection between form and function in bird species, as observed in previous global analyses (Pigot et al. 2020; Tobias et al. 2020). This functional segmentation of the morphological spectrum at the biome level suggests that the geometrical characteristics of functional spaces should be considered in efforts to conserve functional diversity at multiple scales. These characteristics can serve as potential surrogates or indicators of a community's functional integrity (Mouilot et al; 2013; Auber et al. 2022). In our analysis of tropical savanna spaces, we observed that some ecological groups occupy more central positions, while others are distributed mainly along the periphery, indicating variable contributions to the overall functional architecture. Nectarivores, for instance, are predominantly concentrated in the hotspot nucleus of the global functional spectrum, with the notable exception of the Cerrado's nectarivorous species, which form an almost exclusive group, sharing a limited functional space only with Africa's and Australia's invertivores. This suggests that the loss of the Neotropical Trochilidae family could lead to an irreversible erosion of the functional space. Conversely, vertivores and aquatic predators are consistently distributed away from global hotspots, delineating the borders of the functional spectrum in terms of size.

The variations observed in the morphological signatures shaped by trophic niches across different savannas reflect the diverse ecological contexts underlying tropical savanna bird biodiversity. Different functional groups are variably affected by anthropogenic threats, leading to functional shifts within communities that manifest as patterns of erosion in functional structures, with still-unknown ecological consequences (Bełcik et al. 2020; Toussaint et al. 2021). For birds, it is projected that the extinction of threatened species will shift the global pool toward smaller species with shorter life cycles, higher fecundity, and generalist behaviors, often with insectivorous tendencies (Cooke et al. 2019). Before species face complete extinction, their populations undergo successive pressures, leading to local and regional disappearances that already leave functional imprints (Laliberté et al. 2010; Etard et al. 2021). Thus, even before extinction occurs, species' contributions to the structuring of biodiversity are reduced (Carmona et al. 2017). Given that tropical savannas are under significant pressure (Murphy et al. 2016; Buchadas et al. 2022), certain parts of the functional spectrum are likely more threatened than others. Depending on the implications of this scenario of pressures in each savanna, different conservation strategies should be considered to secure bird functional diversity across the tropics, given that each savanna region presents functional structures with different vulnerabilities as a result of their unique biogeographical histories (Corlett and Primack, 2006).

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Capítulo 2

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Functional Vulnerabilities of Bird Diversity to Habitat Loss in a Neotropical Savanna

ABSTRACT

Aim

We investigate the functional diversity of birds in the Cerrado, its distributional patterns and the impacts of native cover loss patterns on its structure. By mapping the spatial interaction between functional diversity and cover loss, we aim to understand how current patterns of savanna occupation compromises bird functional diversity and associated ecological functions.

Location

Brazilian Cerrado.

Methods

We constructed the functional space to describe the diversity of bird assemblages across the Cerrado and evaluated their functional diversity attributes. By mapping this functional data onto the vegetation cover loss data, we assessed a potential state of functional erosion in the Cerrado.

Results

We revealed that functional diversity attributes are unevenly distributed across the Cerrado. Further, on average, Cerrado bird species have 41% of their ranges impacted by habitat loss, leading to varied functional consequences. The spatial pattern of functional redundancy did not fully align with functional richness, indicating distinct species distributions within functional spaces. By examining the spatial interaction between functional diversity attributes and native cover loss, we identify areas with vulnerable functional structures and high conservation potential. This study highlights the necessity for targeted conservation strategies to protect the ecological functions of bird species in the Cerrado.

Main conclusions

Conservation efforts for protecting bird functional diversity across the Cerrado must consider the spatial distribution of key functional attributes. Our research highlights that some regions, based on their functional structure characteristics and the state of native vegetation cover, are more functionally vulnerable than others. Ultimately, our study demonstrates how the functional diversity framework can serve as a tool for conservation planning. Our approach can be adapted to other ecosystems or taxa and be integrated with other ecological community methods to assess the impacts of habitat loss and degradation on the structural frameworks that

describe and support biodiversity and its functional contributions to ecosystems and people.

Keywords: Aves, Conservation planning, Cerrado, functional diversity, Neotropical savannas, biodiversity loss**.**

INTRODUCTION

Savannas are distributed across vast areas of South America, Africa, Asia, and Australia (Archibald et al. 2019). The geographical magnitude of the savanna biome makes it an important biome for the protection of tropical biodiversity (Bond & Parr, 2010; Murphy et al. 2016). However, due to a forest bias in ecosystem protection, savannas and other open formations experience high levels of pressure on their remnants (Pennington et al. 2018; Buchadas et al. 2022). A striking example is the Cerrado, a Brazilian biome that originally covered 2 million km², and has about 50% of its native area converted to anthropogenic land uses, and faces growing deforestation rates higher than those found in the Amazon rainforest (Strassburg et al., 2017; Zalles et al. 2019; Machado & Aguiar, 2023). Aggravating this situation, the protection rates of these two biomes are contrasting, with about 50% of the Amazon formally protected compared to only 14% of the Cerrado (Overbeck et al. 2015; Alencar et al. 2020). Other large savanna regions such as sub-Saharan Africa and northern Australia have not reached the level of occupation seen in the Cerrado (Brink & Eva, 2009; Murphy et al. 2016; Woinarski et al. 2020), but are target of future plans for large-scale agricultural development and biofuel production. This indicates a scenario of intensified anthropogenic advancement over these landscapes, with high costs for global biodiversity and climate (Commonwealth of Australia, 2015; Ordway et al. 2017; Searchinger et al. 2015, Buchadas et al. 2022).

The tropical savanna biomes not only differ in the historical anthropogenic occupation of their native areas, but also in their evolutionary histories (Cole, 1986). This results in savannas such as the ones found in South America, Africa, and Australia, although structurally similar, are composed of unique faunas and floras (Solbrig, 1996), thus differing in their contributions to global biodiversity. An extensively present group in these savannas are birds. It is estimated that 2,951 species (25 orders, 152 families, and 1,404 genera) occur in tropical savannas (Franchin et al. 2008). Birds form species-rich communities adapted to the different strata of vegetation, establishing interactions across multiple trophic levels and playing important ecological roles as pollinators, seed dispersers, and predators (Barnagaud et al. 2019; Tobias et al. 2020). The aspect of biodiversity associated with the ecological roles of species is known as functional diversity, and its study highlights that the global crisis of species loss has consequences beyond the taxonomic dimension. In other words, the loss of species in response to global pressures such as habitat loss results in the loss of ecological strategies associated with the maintenance of ecosystem functions (Cooke et al. 2019).

A prominent way to study functional diversity is through the construction of multidimensional spaces, where each dimension represents a functional trait of interest, and species are distributed according to their respective values (Villéger et al. 2008). This approach allows for the identification of the functional structure emerging from communities, which can be analyzed both in terms of their boundaries and patterns of occupation (Carmona et al. 2019). Mapping the diversity in these functional spaces enables the analysis of how the functional structure supported by a group's diversity has varied historically and how this structure may continue to change according to observed or projected patterns of species loss (Germain et al. 2023). Global projections of threatened species extinction reveal a scenario not only of ecological strategy loss but also of pervasive erosion of the functional spectrum through the isolation of species in the functional space, deepening ecosystems vulnerability to eventual extinctions (Carmona et al. 2021; Cooke et al. 2019).

In the specific case of birds, it is projected that the extinction of threatened species will shift the global pool towards a pattern of smaller species with faster life cycles, high fecundity, and generalist habits with insectivorous tendencies (Cooke et al. 2019). The overall effect of species loss on the global functional structure of birds is buffered by the aggregated distribution pattern of these species in the global functional spectrum (Carmona et al. 2021). This pattern is maintained when the same analysis is repeated separating the main biogeographical region of the world. In the case of bird functional diversity, the aggregated pattern on the global functional realm (Pigot et al. 2020) again alleviates the regional partitioning of the impact of species loss by showing similar occupation of the spectrum and consistent functional losses among biogeographic regions (Toussaint et al. 2021).

Having a functional structure robust to the global pattern of species loss is important from an evolutionary perspective, however, from an ecological one, a closer look on spatial patterns of functional degradation may be needed to identify functional vulnerabilities of regional faunas and conservation strategies to respond to them. Mapping how the functional structure will respond to species extinctions allows us to visualize the most extreme scenario of functional impact. However, before species become completely extinct from the biosphere, their populations go through a succession of negative pressures, disappear locally and regionally, already imprinting functional consequences (Laliberté et al. 2010; Etard et al. 2021). Thus, before the final impact of extinction, species have their relative contributions to the structuring of this diversity reduced due to a decrease in their incidence in their distributional range (Carmona et al. 2017). This preliminary functional impact will be differentially distributed across a biome’s extent, and identifying where properties of functional diversity are being most impacted may help target actions that are most likely to protect the ecological functions performed by species in the geographical space and the overall structure that secures this diversity and associated functions in the functional space.

In this study, we map the impacts of habitat loss on the functional diversity of birds in a tropical savanna that faces intense native vegetation conversion pressures, the Cerrado. We focus on properties such as functional richness, functional redundancy, functional evenness and functional divergence, as they represent important characteristics informing functional diversity (Manson et al 2005). Our main goal is to assess functional vulnerabilities and guide the direction of conservation actions tailored for the nature of the functional vulnerability identified. We repeat this assessment for birds categorized in ecologically important groups of trophic niche: frugivores and insectivores. Our goal with this ecological representation is to map the spatial distribution of the diversity structure most likely associated with the provision of species related ecosystems services and how patterns of savanna occupation may be jeopardizing it. We hope that our results can aid in directing conservation actions for tropical savanna birds, focused on building resilience to the functions provided by the multiple species inhabiting and shaping the ecosystems of this distinct and important tropical biome.

METHODS

Study Area

The study area is the Cerrado, a neotropical savanna located at the central portion of Brazil, covering approximately 2 million km^2. The Cerrado is characterized by a mosaic of grasslands, shrublands, and forests, supporting a unique array of flora and fauna, with high levels of endemism, rendering it the biodiversity hotspot classification. Specifically, the geographic boundary used here is the Cerrado represented in the "Tropical & Subtropical Grasslands, Savannas & Shrublands" biome category obtained from the updated Ecoregions of World dataset presented in Dinerstein et al. (2017).

Species data

The lists of bird species occurring in the Cerrado were compiled in two stages. First, an advanced search was conducted on the IUCN website (https://www.iucnredlist.org/) to filter the global list of extant bird species recorded in each South America, then the geographic distribution file was downloaded for each species. IUCN's birds maps are from BirdLife International (http://www.birdlife.org/datazone/home) and represent the breeding range of the species. From this initial list, a spatial filter was applied between the savanna boundaries and the geographic distributions of the listed species. Thus, species whose distributions overlapped with the Cerrado's boundaries were retained in the species list. We note that distribution maps have limitations associated with their coarse resolution and susceptibility to overestimating presences, but they represent the best available data for generating species composition in scales such as ecoregions and reduce the effects of detection differences and over/under-sampling (Cooke et al. 2019).

Further, the Cerrado region was segmented using a regular grid of cells measuring 1 x 1 degrees. This grid was used as the basis for the spatial systematization of species occurrences across the biome. An incidence matrix was produced indicating presence/absence of species in each grid cell. Due to the coarse nature of the data, no cutoff value was used for the definition of presence or absence.

Functional diversity

The functional traits used here represent linear morphological measurements. Thus, the functional variation considered in this study directly relates to morphological aspects of species. Linear measurements, although they do not geometrically capture the shape of species, have the advantage of being easily recorded. This allows for linear measurements of species from different sources to be gathered with less risk of error. Our functional trait data were obtained from the AVONET database (Tobias et al., 2022), which represents a compilation of individual-level measurements for all extant bird species worldwide aggregated in a standardized manner at the species level. Among the information included in the database are nine linear morphological traits, including four bill measurements, three wing measurements, tarsus length, and tail length (Figure 1). The choice of morphological characters is based on their established associations with relevant ecological aspects for bird species such as diet, dispersal, and locomotion (Leisler & Winkler, 1985; Miles & Ricklefs, 1984; Pigot et al., 2020; Ricklefs & Travis, 1980).

Bird diversity will also be considered in ecological categories based on diet data (Wilman et al., 2014; Tobias & Pigot, 2019) indicating the trophic niche classes of frugivores and insectivores. These classes were chosen due to their high level of diversity and important ecological functions performed by their representatives.

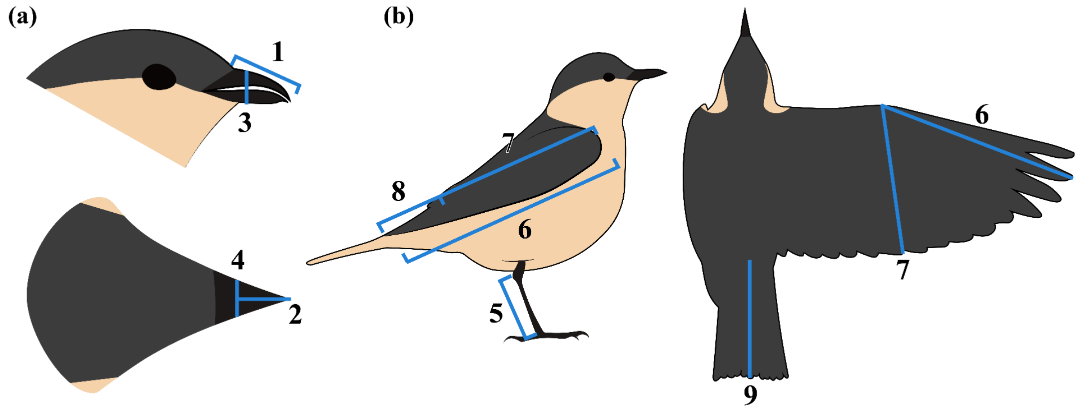

Figure 1. Illustration of the morphological characters compiled in the AVONET database (Tobias et al., 2022). a) Beak measures; b) Body measures. Figure is based on an original illustration by Richard Johnson published in Pigot et al. (2020). Adaptation by Isabella Silveira.

Multidimensional functional spaces

The representation of the functional structure of bird diversity in each savanna will be achieved through the construction of a functional space. By selecting continuous traits, it is possible to construct a functional space where each axis represents the variation observed in a trait (Villéger et al. 2008). Before any analysis, these traits were transformed and scaled to have a mean of zero and a standard deviation of one (Palacio et al. 2022). The functional spaces are built from a Principal Component Analysis (PCA) of the Euclidean distances between species. The proposed surface will represent a dimensionally reduced functional space composed of the main axes of morphological variation of the bird communities in each cell of the regular grid segmenting the Cerrado. The dimensionality of this space will be identified through a Horn's parallel analysis using the `paran´ package (Dinno, 2018) and a significance test of PCA using the `PCATest´ package (Camargo, 2022). The retained axes will define the functional space from which the distribution probabilities of species will be estimated. This probabilistic surface, constructed based on multivariate kernel density analyses, will describe the distribution of traits values probabilities (hereafter TPDs) and will serve as the basis for analyses of the functional impacts of habitat loss (Carmona et al. 2019).

Estimating the Trait Probabilities Density functions

TPDs are probability density functions that reflect the likelihood of observing species with specific combinations of functional traits values within the defined functional space. Therefore, a TPD allows the mapping of the functional space as a probabilistic surface that can be analyzed both for its boundaries and for its occupancy pattern (Carmona et al. 2016). The TPDs will be defined by functions from the `TPD´ (Carmona et al. 2019) and `ks´ (Duong , 2007) R packages.

With the estimated TPDs, their surfaces will be divided into a regular D-dimensional grid. Thus, its continuous variation will be categorized, and a TPD function value will be calculated for each TPD cell (Carmona et al. 2019). The TPD value in each cell represents the density of species in that particular area of the functional space. That is, the number of functionally similar species. The number of grid cells will be defined *a priori* and will depend on the dimensionality of the space. Following Toussaint et al. (2021), two-dimensional spaces can be divided into 40,000 cells of 200 x 200 units and maintain the functional variation representation. Given their probabilistic nature, TPDs will graphically have their contours containing 50 and 99% of the total probability graphically highlighted, emphasizing the areas of higher species concentration and excluding outliers from the distribution in the delimitation of functional space borders.

The TPDs from all species co-occurring in grid cells will be combined representing the probability density function of the assemblage (Carmona et al. 2019). This step will be repeated for the assemblages of frugivorous and insectivorous species. As a result, each grid cell will have its own estimated functional structure associated with its species assemblage.

Functional diversity indices

The quantification of the functional diversity of the bird fauna in each studied tropical savanna region will be based on the approach of continuous traits (Magneville et al. 2022). That is, functional diversity will be measured from the n-dimensional morphospace represented in the TPDs. The following multidimensional indices of functional diversity were calculated: functional richness, functional redundancy, functional evenness and functional divergence, all of which were calculated using the functions of the \`TPD´ package (Carmona et al. 2019).

Functional richness quantifies the volume or area of the TPD encompassing all species present in the functional space, representing the proportion of the total functional space occupied or the diversity of functional combinations present in the community (Cornwell et al. 2006; Villéger et al. 2008; Carmona et al. 2019). Functional redundancy, represents the number of functionally similar species (Carmona et al. 2016). Functional evenness is an indicator of regularity in the distribution of abundance within the occupied trait space. Evenness ranges from 0 to 1, with values close to 1 indicating that trait values have similar probability distribution, and values close to 0 indicating aggregated irregular cell probabilities in the functional spectrum (Carmona et al. 2019). Finally, functional divergence measures to what extent trait values near the center of gravity of the functional volume are more or less dense than trait values at the extremes (Carmona et al. 2019). Divergence also ranges from 0 to 1, and the indice approaches 0 when the most abundant trait values are close to this center, and approaches 1 when the most abundant trait values are furthest away. Ecologically, functional evenness and divergence may represent how niche space is occupied within groups.

Characterization of native cover loss in savannas

To characterize the loss of native cover in tropical savannas, we utilized the deforestation archetype product by Buchadas et al. (2022). This product characterizes the deforestation frontiers of non-forest tropical biomes into archetypes that differ based on the patterns of native vegetation conversion (Figure 2). Since the objective of the present study is to characterize vegetation loss, the six archetypes described by Buchadas et al (2022) were unified into a single class representative of native vegetation loss. Within each spatial grid cell, we registered the total area occupied by native vegetation loss activities. Using this information, we illustrated the degradation status of the non-forest vegetation within each cell. The higher this value, the greater the area of savanna cover already occupied by erosive processes in the region.

Impacts of deforestation on functional diversity

The potential impact of native cover loss pressures in the Cerrado on the functional diversity of birds will be assessed by the bivariate choropleth maps that allow the observation of the spatial interaction of two or more variables simultaneously. Each functional diversity index and the savanna occupation values were divided into three mean quantile groups representing low, medium and high values within their distributions. Each grouped functional metric interacted with the grouped values of native vegetation cover loss and were plotted in a nine colors legend system.

RESULTS

Distribution of bird diversity indices

Taxonomic Diversity

The Cerrado was divided into 255 cells of 1 x 1°. The values of taxonomic richness for the assemblages defined in each grid cell ranged from 279 species to 630 species, with an average of 429 species per cell.

Considering only the trophic niche groups, frugivorous taxonomic diversity was of 136 species and grid assemblages ranged from 13 to 72 species, with an average of 37 species per grid cell. A total of 589 insectivorous species were listed, and assemblages ranged from 133 to 318 species, with a mean of 209 species per grid cell.

Functional Diversity

The Cerrado showed functional richness values ranging from 81.36 to 95.63, with an average of 88.20 per grid cell. Functional redundancy values varied between 0.072 and 0.090, averaging 0.082. Functional evenness was recorded from 0.49 to 0.53, with a mean of 0.51. Finally, functional divergence ranged from 0.45 to 0.53, with an average of 0.50.

For the trophic niche groups, frugivorous species exhibited functional richness between 21.70 and 49.31, while insectivorous species ranged from 51.70 to 64.90. Functional redundancy for frugivorous species ranged from 0.060 to 0.163, and for insectivorous species, it ranged from 0.122 to 0.150. Functional evenness values for frugivorous species were between 0.54 and 0.68, and for insectivorous species, they ranged from 0.46 to 0.53. Lastly, functional divergence for frugivorous species varied from 0.63 to 0.76, while for insectivorous species, it ranged from 0.44 to 0.51.

Functional diversity attributes of all species assemblages and trophic niche groups were classified into three groups based on mean quantiles, representing intervals of low, medium, and high values (Table 1).

Table 1. Functional indices values categorized by mean quantile groups for all species and across different trophic niche assemblages.

Assemblages	Levels	Functional indices			
		Richness	***Redundancy***	***Evenness***	***Divergence***
All Species	*Low*	81.35 - 86.37	0.072 - 0.081	0.49 - 0.51	0.45 - 0.50
	Medium	86.37 - 88.72	0.081 - 0.084	0.51 - 0.52	0.50 - 0.51
	High	88.72 - 95.63	0.084 - 0.090	0.52 - 0.53	0.51 - 0.53
Frugivorous	*Low*	21.70 - 35.46	0.060 - 0.077	0.54 - 0.63	0.63 - 0.68
	Medium	35.46 - 38.12	0.077 - 0.092	0.63 - 0.65	0.68 - 0.71
	High	38.12 - 49.31	0.092 - 0.163	0.65 - 0.68	0.71 - 0.76
Insectivorous	*Low*	51.70 - 55.16	0.122 - 0.133	0.46 - 0.49	0.44 - 0.47
	Medium	55.16 - 57.19	0.133 - 0.139	0.49 - 0.50	0.47 - 0.48
	High	57.19 - 64.90	0.139 - 0.150	0.50 - 0.53	0.48 - 0.51

Distribution of native cover loss impact on species ranges

On average, Cerrado's cells were 43% occupied by the erosive process represented by the combination of the deforestation archetypes identified by Buchadas et al. (2022). The mean quantiles intervals classifying degree of native cover loss within cells were: Low: 0 - 32%; Medium: 32 - 54%; High: 54 - 99%. Birds' distribution on average encompassed 36% of the biome and had an average of 41% of their ranges impacted by native cover loss. We note that this average represents the total amount of native area converted within a species' range, and does not consider the spatial pattern of such loss.

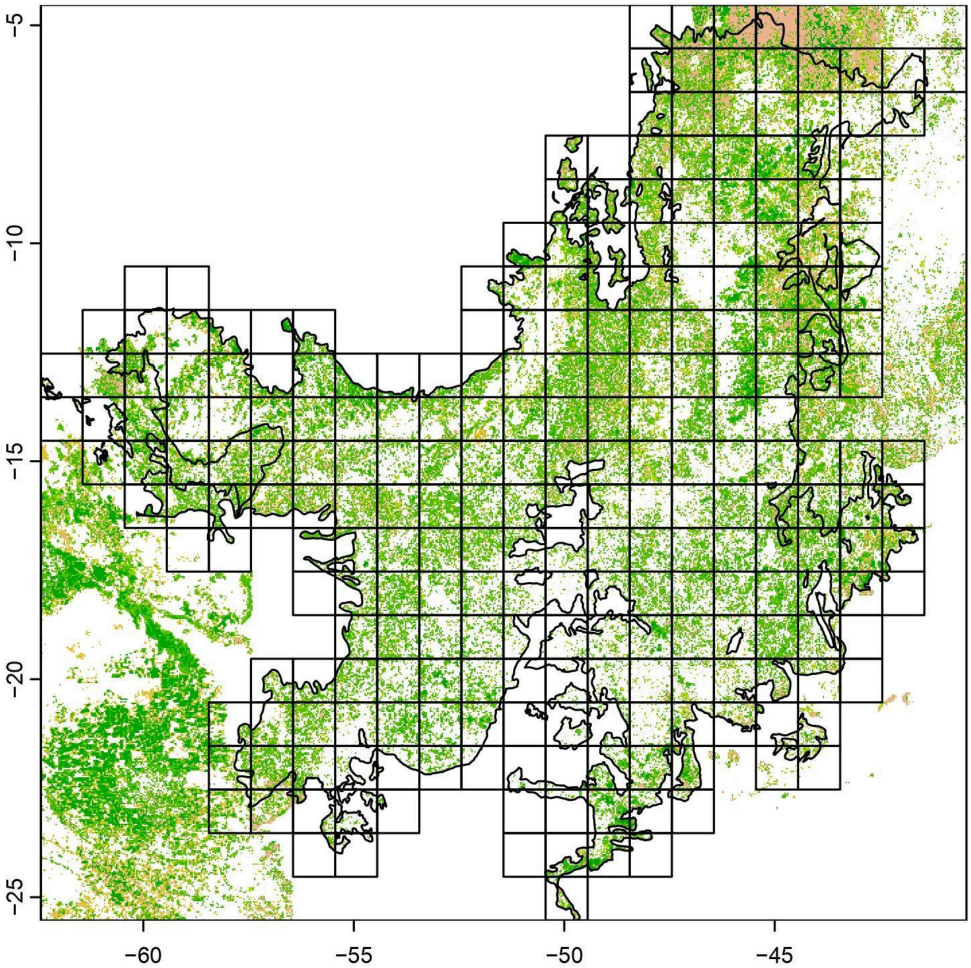

Figure 2. Representation of the archetypes of native loss within the study region. Deforestation data was taken from Buchadas et al. (2022). Different colors in the legend represent the six different archetypes identified by Buchadas et al. (2022). For the purpose of this study, we dissolved the archetypes and worked with a unified class of habitat conversion.

Distribution of functional diversity values

Focusing on cells transitioning from bright blue to dark gray and light gray to bright red, we identify areas with high and low values of their respective functional indices (Figure 3). The blue areas of high functional richness are located in the western portion, where the Cerrado begins to transition to the Amazon forest and in the southeast border where the Cerrado transitions to the Atlantic Forest. The functional redundancy spatial pattern does not completely match the functional richness one (Figure 3). The Cerrado-Amazon transition zone has variable values of redundancy, whereas the southern Cerrado-Atlantic Forest border seems to be a region with high levels of functional richness and functional redundancy (Figure 3).

The high levels of functional richness in the western border are accompanied mostly by low levels of functional evenness and functional divergence (Figure 3). This indicates that in these functional rich regions, species are aggregated and close to the center of gravity of the functional space. Functional divergence and evenness seem to peak at the lower and central portions of transitions between the Cerrado and Atlantic Forest (Figure 3). This indicates regions where there is presence of extreme trait values, but the occupation of the functional space is more evenly distributed.

Interactions of native cover loss and functional diversity

Now considering the state of native cover conversion within cells, we note that, because different aspects of functional diversity are differently distributed along the Cerrado, their interactions with habitat loss pressures show distincts geographical footprints (Figure 3). Note that some regions will have a low deforestation area because of the base data of savanna vegetation within the cell. As such, low values of native cover conversion may also mean low savanna area in the grid cell. It does not mean that the savanna within the cell is necessarily in a good conservation state. These cells are mostly the ones located in the regions where the Cerrado borders forest biomes (Figure 2). For this reason, for the results of interaction of devegetation and functional diversity, we will focus on cells with significant presence of savanna captured by the Buchadas et al (2022) dataset (See Figure 2 for visual reference).

Dark gray regions on the map represent areas with high values of functional diversity indices and of vegetation erosion (Figure 3). Conversely, light gray areas indicate comparatively low values of functional diversity indices and of native vegetation conversion (Figure 3). Mapping these dark gray areas for functional richness and redundancy is an important task because of what these functional indices mean. Functional rich areas are regions that secure a comparatively larger number of ecological strategies, and regions of high functional redundancy are where the represented ecological strategies are theoretically more ecologically ‘insured’. These indices can be considered together for conservation action. Dark gray cells of functional richness show areas where diverse ecological strategies are threatened by habitat loss. Depending on the species distribution within the functional space and their redundancy levels, these regions may face irreversible damage to their functional structure. In the northern part of the Cerrado, where high devegetation values coincides with low functional richness and redundancy (bright red areas in Figure 3), the erosion of functional diversity is likely happening at an accelerated pace.

Impacted areas of high values of functional richness and functional evenness can be targeted to conserve a greater range of ecological strategies, with conservation actions that aim to secure the density distribution within it, by also protecting intermediate trait values. Impacted areas with high functional richness and high levels of functional divergence may be the focus for conservation strategies focused on protecting large portions of the Cerrado functional spectrum and extreme traits in assemblages where these less predominant traits are more present. All strategies above cited could be combined with functional redundancy as a way of prioritizing areas most vulnerable to species loss (i.e. areas of low redundancy). These are just a few examples on how regional systematic conservation planning of areas could be planned with the protection of the functional spectrum in mind.

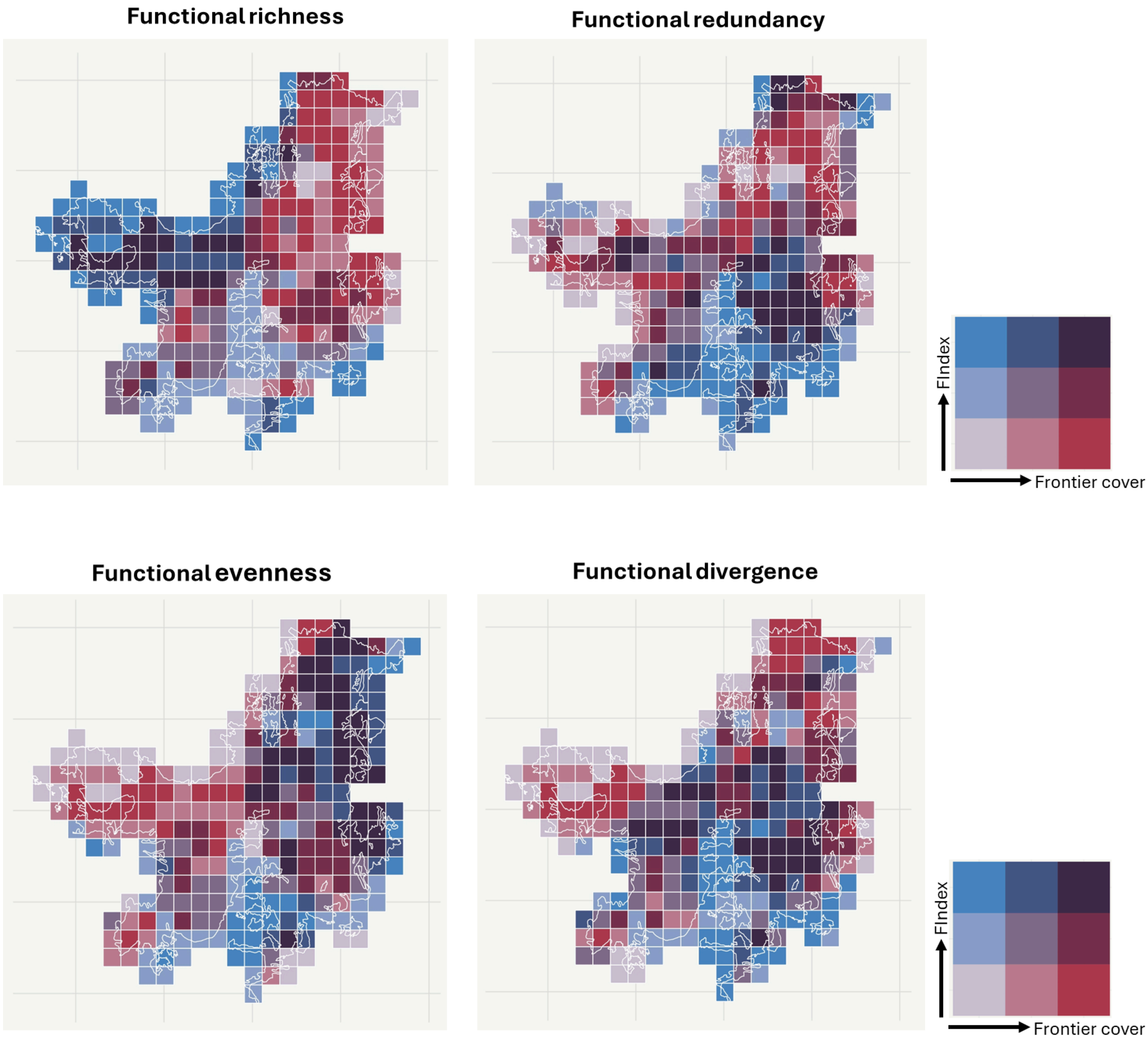

Figure 3. Distribution of native cover conversion pressure on the functional diversity of birds in the Cerrado. Values of functional richness, functional redundancy, functional evenness and functional divergence are represented. Colors indicate the interaction between functional indices and cell occupation by deforestation.

Potential impact of native cover loss on species' ecological functions

Beyond the protection and conservation of the hypervolume characteristics defining a group's functional diversity, conservation action for functional diversity may also have the goal of halting or reducing the loss of ecological function (Cadotte et al. 2011). The morphological approach to functional diversity applied here does not always map on to ecological function, but the role of evolutionary convergence on bird traits combinations established a connection between form and function for this group, which validates the use of morphological traits as a framework for assessing the functioning of avian communities (Tobias et al. 2020).

As a way of demonstrating the impact of native cover loss on ecological functions provided by species, we assessed the specific case of frugivorous (Figure 4) and insectivorous (Figure 5) birds, trophic niches which species act as potential providers of the ecosystem services of seed dispersal and of pest suppression, respectively (Whelan et al. 2008, Gaston et al. 2022). High functional richness for frugivore diversity was found in the Amazon-Cerrado border, only coinciding with high values of redundancy in the far western tip of this transitional region. Frugivore redundancy was also expressive in the transition between the Cerrado and Atlantic Forest (Figure 4). The northeastern portion of the Cerrado presented areas of high values of native cover loss and of concomitant low values of functional richness and redundancy, indicative of a functionally vulnerable region (Figure 4). Functional evenness values were more variably distributed across the biome, with many regions of intermediate values. Most notably, the Cerrado-Amazon border of high functional richness corresponds to a region with low values of functional evenness and divergence. Finally, the southeast of the Cerrado appeared as a region of low functional richness and high divergence for frugivores.

For insectivores, functional richness and redundancy presented contrasting spatial patterns, except in the central portion where the Cerrado transitions to Atlantic Forest, and where cells of intermediate functional richness present significant levels of redundancy (Figure 5). Northern portions of the biome concentrate region of low functional richness and intermediate to high levels of native cover conversion (Figure 5). Intermediate values of savanna occupation might indicate regions where the deforestation frontier have not yet settled. Among those cells, the transition between Cerrado and the Dry forests of Caatinga in the northeast presents a region of low insectivore functional richness but of high redundancy and evenness (Figure 5). Indicating possible stable functional structures. The northern region of Cerrado presented cells of high levels of divergence and of high native cover conversion values (Figure 5). Indicating areas where extreme traits are being disproportionately impacted by habitat loss.

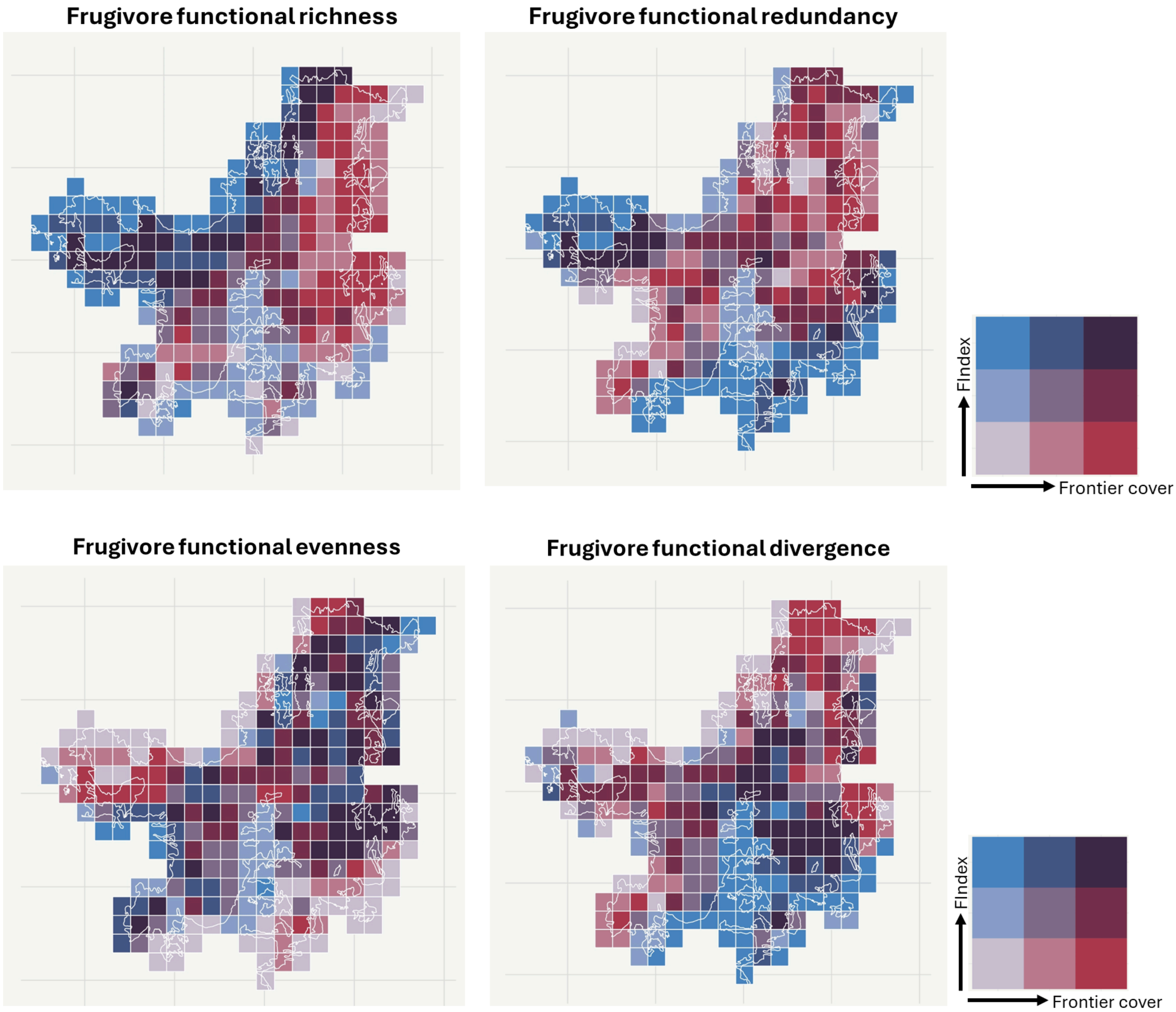

Figure 4. Distribution of native cover conversion pressure on the functional diversity of frugivorous birds in the Cerrado. Values of functional richness, functional redundancy, functional evenness and functional divergence are represented. Colors indicate the interaction between functional indices and cell occupation by deforestation.

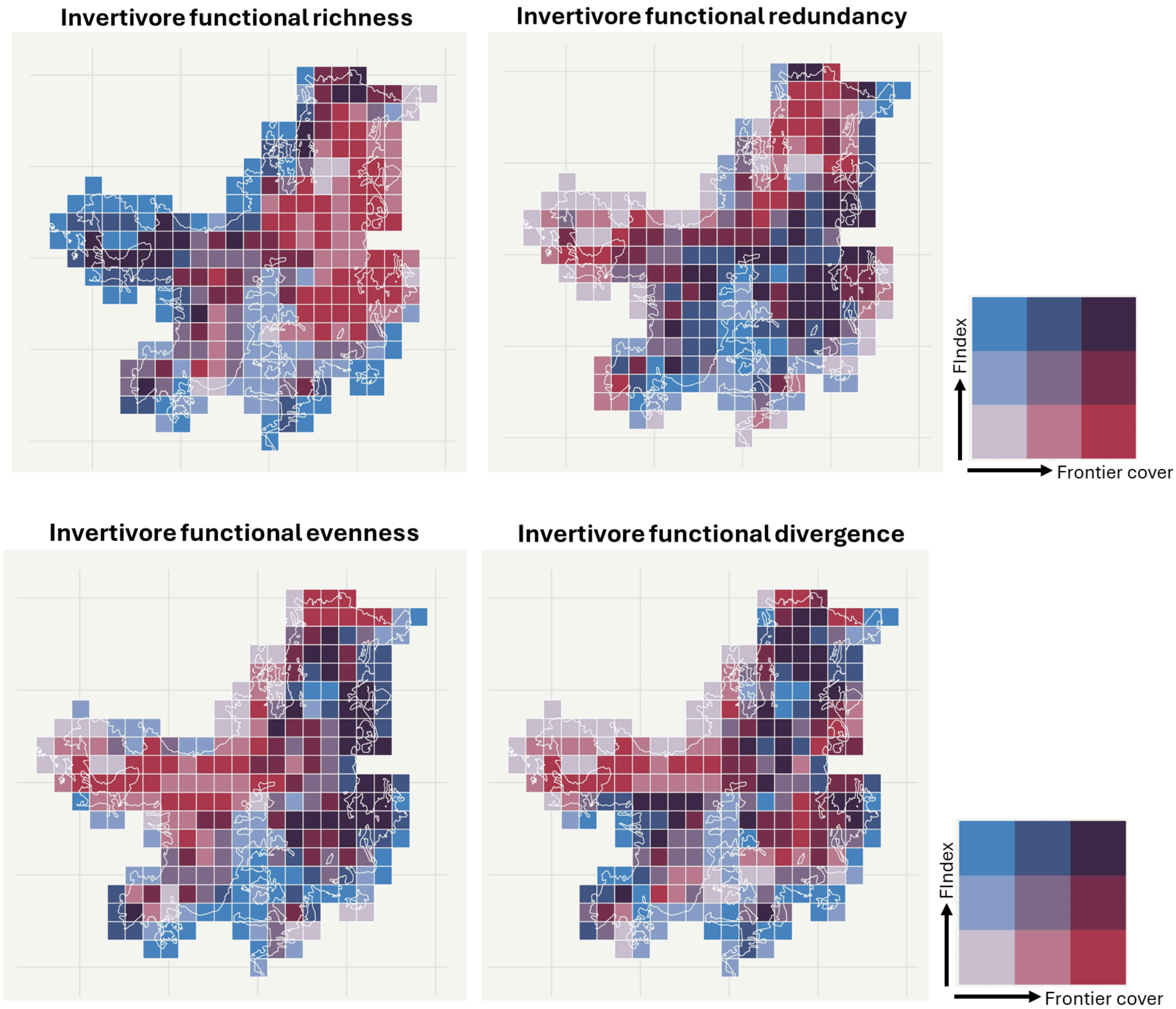

Figure 5. Distribution of native cover conversion pressure on the functional diversity of insectivorous birds in the Cerrado. Values of functional richness, functional redundancy, functional evenness and functional divergence are represented. Colors indicate the interaction between functional indices and cell occupation by deforestation.

DISCUSSION

In this study, we estimated the functional structures emerging from the potential species assemblages distributed across the Cerrado and assessed their values of functional richness, redundancy, evenness and divergence. We mapped the spatial interaction of the functional indices to native cover loss patterns and obtained a static picture of the state of functional erosion of bird diversity caused by habitat loss in the Cerrado. Bird diversity in the Cerrado and their functional attributes are differently distributed across the biome. This has consequences to the spatial planning of conservation actions focused on protecting biodiversity and associated functions or services (Conole and Kirkpatrick, 2011; Ferraz et al. 2014). Our study shows that Cerrado's species have, on average, 41% of their ranges impacted by native cover loss, which results in different functional consequences for the overall functional structure supporting this biodiversity. We note that this is the total amount of native area converted within a species' range, and does not consider the spatial pattern of such loss that, depending on the configuration, may buffer or deepen habitat loss' functional impacts (Karimi et al. 2021; Martello et al. 2023).

We showed that, for the studied Cerrado bird diversity, the spatial pattern for functional redundancy values did not completely match that of functional richness. This is a noteworthy result because of the positive correlation these two functional metrics are known to have (Mouillot et al 2014). The more species present in a sample, the greater the likelihood of encountering new trait values and having these traits represented by multiple species. We reduced this relationship by dividing redundancy values by the total number of species minus one, so that redundancy is expressed in relative terms and in proportions (Carmona et al. 2019), but this correspondence was not neutralized. Therefore, the contrasting spatial patterns of functional richness and redundancy informs on how species are distributed within the functional space. The two metrics most related to species distributions within the functional space are functional evenness and divergence (Mouillot et al., 2005; Schleuter et al., 2010). Evenness measures how regularly the probabilistic hypervolume is shaped, whereas divergence measures how species are spread across the functional space, with higher values indicating more species with contrasting traits (Mason et al., 2005; Villéger et al., 2008; Anderson, 2006; Carmona et al. 2019).

Our results indicated that, on average, Cerrado's cells were 43% occupied by erosive processes. Across this widespread scenario of native vegetation suppression, we mapped where high devegetation overlapped with functional diversity attributes to assess the potential functional impacts incurred by the patterns of occupation of Cerrado's landscapes. We argue that each functional attribute represents hypervolume characteristics that can be translated into communities' functional potentials and vulnerabilities. By examining the spatial interaction between these functional attributes and native cover loss, we can identify regions most in need of conservation attention, both in terms of restoration and of protection of their current state due to large diversity potential (Tscharntke et al. 2005; Brasileiro et al. 2022). Depending on the functional characteristics of interest, such as protecting regions holding more ecological strategies (i.e., higher functional richness), regions containing extreme trait values (high functional divergence), regions with efficient resource use (i.e., high functional evenness), or combinations of these attributes, functional redundancy can be used to guide the direction of conservation action in areas of different functional potentials. Areas of low redundancy, and concomitant high rates of native vegetation conversion, indicate regions with vulnerable functional structures (Carmona et al. 2016), whereas areas of higher functional redundancy may represent more robust functional structure characteristics (Rosenfeld, 2002).

Beyond the protection and conservation of the hypervolume characteristics defining a group's functional diversity, conservation actions may also have the goal of halting or reducing the loss of ecological function (Cadotte et al. 2011). The morphological approach to functional diversity applied here does not always map on to ecological function, but the role of evolutionary convergence on bird traits combinations established a connection between form and function for this group, which validates the use of morphological traits as a framework for assessing the functional contributions of avian communities, specially when considering ecological groups such as of trophic niche (Tobias et al. 2020).

When applying the functional diversity framework used here to ecosystem service provision, each functional index could represent different contributions. Functional richness within a trophic group indicates more trait combinations performing similar functions, broadening the spectrum and scale of service provision (Brasileiro et al. 2022). For example, this could result in a greater variety of seeds being dispersed across different ranges and environments, or more types of invertebrates being consumed in various environments and at different times of the day. Functional evenness and divergence may act as complementary information to richness' effect on service provision. Functional evenness within assemblages of species of the same trophic niche may indicate a more distributed use of the available resources, whereas functional divergence may suggest areas where the ecological functions provided by species with more extreme traits are more prevalent. Combined, these indices assess regions with assemblages that present different characteristics of resource use and, consequently, associated ecological functions potentials of provision and support systems (Kramen, 2005). While assumptions on the relationship between functional structure and ecological function need empirical testing (Luck et al., 2012; Diaz et al., 2013), assessments like ours can guide conservation efforts to impacted areas with vulnerable functional characteristics.

The aim of our study was to incorporate the multidimensional approach used to study functional diversity into the toolbox of spatial conservation planning, using the Cerrado's birds as a study example. Before generalizing our observations or applying them to inform finer scale conservation decisions, some limitations should be noted. The first limitation concerns the base data used to represent native area conversion. The archetypes of deforestation produced by Buchadas et al. (2022) aimed to map areas of deforestation in tropical woodlands. Consequently, the authors considered all forests, shrublands, and savannas within two biomes according to the updated biome classification of Dinerstein et al. (2017): (1) tropical and subtropical dry broad-leaved forests and (2) tropical and subtropical grasslands, savannas, and shrublands. When the regular grid was applied to the Cerrado's extent, transitional regions of savanna to other biomes had no data on deforestation. This omission resulted in notably low values of deforestation identified in regions such as the Cerrado-Amazon border, also known as the "arc of deforestation," an area known for high levels of habitat degradation and land conflicts (Lapola et al. 2014). In such regions, our maps do not accurately reflect the reality of the functional impacts of native cover loss.

Another limitation of our study is the coarse nature of the geographical range data used to represent species occurrences and to build the unweighted TPDs. We used the assemblage of species co-occurring within grid cells as a proxy for an ecological community, meaning that no abundance data was used to weight species contributions to functional structure, which is common for larger-scale studies (Cooke et al. 2019a, Carmona et al. 2021, Toussaint et al. 2021). Consequently, classical interpretations of functional indices such as functional evenness and functional divergence had to be adapted (Villéger et al. 2008; Carmona et al. 2019). Additionally, by not including abundance data, we could not directly measure the impact of habitat loss on the relative contributions of species or assemblages to the functional structure. Future studies can explore these ideas with more detailed datasets to identify areas of the functional spectrum most vulnerable to reductions in species contributions, enabling the development of functional restoration strategies. Furthermore, our approach can be adapted to finer spatial scales, other ecosystems and taxa and could be used in conjunction with other ecological community approaches, such as ecological network analysis (Carvalho et al. 2023), to assess how habitat loss and degradation imprint their consequences in the architectural structures describing and supporting biodiversity and its functional contributions to ecosystems and people.

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Capítulo 3

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Applying the duality concept to functional and geographical spaces in conservation planning

ABSTRACT

We apply Hutchinson's Duality to geographical and functional spaces to study the impact of spatial threats, such as habitat loss, on the functional diversity of Cerrado's birds. Hutchinson's Duality is extended to functional diversity by establishing the mutual relation between the multidimensional space describing functional variation among species and the geographical space defined by species distributions. We achieved this by segmenting each space into cells (i.e., geographical cells and functional cells) that linked their respective functional and spatial information, allowing for the mapping of functional information onto the geographical space and vice versa. Our analysis reveals that only 32.2% of the functional spectrum is occupied by Cerrado bird functional diversity, with functional cells describing trait combinations presenting distinct geographical signatures. Many functional regions displayed high levels of vegetation loss, indicating the widespread state of spatial threats in the functional spectrum. By assessing the functional cells most impacted by habitat loss, we identify the portion of the functional space most likely to trigger a process of functional erosion in the Cerrado's bird diversity and map the geographical locations where conservation action is needed to prevent it. Therefore, our study highlights the potential of functional diversity analysis for spatial conservation planning, showing the value of integrating trait-based knowledge into conservation strategies, and offering a systematic method to address the biodiversity loss crisis in the Cerrado.

INTRODUCTION

Hutchinson in one of his many brilliant theoretical elaborations on the niche concept, presented the idea of a reciprocal correspondence between the niche space and the biotope (Hutchinson, 1978). The niche space is the area or volume delimited by the axes defining the n-dimensions used to describe it, and the biotope was what Huchtinson called the geographical manifestation of ecosystems, which could be defined as any segment of the biosphere with delimited boundaries (Hutchinson, 1957). Since the n axes used to describe a niche are measured in a given space and time, a relationship between the niche and geographical realms is established. This idea, known as the "Hutchinson's duality," enables the mapping of niche information onto the geographical space and vice versa, opening space for many applications that go beyond the niche itself (Cowell and Rangel, 2009). Some examples of applications are the use of climatic variables to map environments, life zones or biomes, and the theoretical rationale behind species distribution modeling (Whittaker, 1967; Nakamura and Soberón, 2009). Basically this concept allows for the study of the geographical signatures of multidimensional spaces defined by their environment.

Species and ecological communities can also be described by multidimensional spaces as it is commonly done in functional diversity studies (Villéger et al. 2008; Magneville et al. 2022; Palacio et al. 2022). Functional diversity is a component of biodiversity that characterizes life in terms of the diversity of functions, and its study focuses on analyzing communities based on the roles played by their organisms (Petchy & Gaston, 2006; Malaterre et al. 2019). The sample unit shifts from species to functional traits that can be described as phenotypical entities such as morphological, physiological, phenological, or behavioral characteristics (Violle et al., 2007; Volaire et al. 2020). Thus, the same way one can define an area by its environmental conditions, one can define a species by its functional traits. Furthermore, since species are not abstract concepts but are geographically rooted by their occurrences or distributional ranges, this enables the transferability of the duality concept to the functional space.

Range information has been applied to large-scale studies on the functional impact of species extinctions, using species geographical distributions to compile global or regional species lists (Carmona et al. 2021; Cooke et al. 2019; Toussaint et al. 2021; Germain et al. 2023). These studies primarily map how functional spaces would respond to species extinctions. However, by shifting the focus from functional space to geographical space and by examining the geographical distribution of trait values, we can assess spatial properties of the functional space of interest, similarly to the concept of geography of climate presented in Coelho et al. (2023). This allows us to map the impacts of geographical threats, such as habitat loss, onto the functional space, identifying functional regions most vulnerable and in need of conservation attention on the ground. This approach also shifts the emphasis from species to functional traits, making it suitable for multi-species conservation planning.

Here, we apply the idea of duality to geographical and functional spaces to study the functional impact of vegetation loss patterns in the Cerrado on bird diversity. Species were represented by 9 linear morphological measurements available at the AVONET database (Tobias et al., 2022). For birds, morphology has established associations with relevant ecological aspects of species such as diet, dispersal, and locomotion (Leisler & Winkler, 1985; Miles & Ricklefs, 1984; Pigot et al., 2020; Ricklefs & Travis, 1980). Further, we segmented the Cerrado into geographical cells of 1º x 1º, and the assemblage of species present in each cell was registered. Adapting Coelho et al. (2023) analysis of climate, we calculated for all geographic cells the mean values of each morphological trait used to describe species and used those averages in a principal component analysis (PCA). The first two axes of the PCA were used to define a two-dimensional orthogonal functional space depicting the distribution of ecomorphological variability of Cerrado's birds assemblages. This functional space was then segmented into functional cells of equal intervals. In this context the Hutchinson's duality applies: A functional cell can represent one or more spatial locations that fall within a specific functional interval, but a geographic cell can only belong to a unique functional cell. With the principles of Hutchinson's duality met, we mapped functional information onto the geographical space to assess the distribution of trait values across Cerrado, and the geographical information of total total native area within functional cells and total area of native area converted to the functional space to assess threatened functional regions.

From applying the duality concept to geographical and functional spaces we hope to demonstrate the potential for this analysis in the fight against biodiversity loss. By transferring functional information back to the geographical area, we can include aspects of functional diversity conservation in large scale multi-species conservation planning and further increase conservation gains by combining different biodiversity analysis techniques.

METHODS

Study area

The study area is the Cerrado, a neotropical savanna located in the central portion of Brazil covering approximately 2 million km². The Cerrado is characterized by a mosaic of grasslands, shrublands, and forests, supporting a unique array of flora and fauna, with high levels of endemism, deeming it a biodiversity hotspot. Specifically, the geographic boundary used here is the Cerrado represented in the "Tropical & Subtropical Grasslands, Savannas & Shrublands" biome category obtained from Dinerstein et al. (2017).

List of species

The species lists for each studied tropical savanna region were compiled in two steps. First, an advanced search was conducted on the IUCN website (https://www.iucnredlist.org/) to filter the global list of extant bird species in South America. For each species included in the study, the geographic distribution file was downloaded. The distribution maps are sourced from BirdLife International (http://www.birdlife.org/datazone/home) and represent the breeding distribution area of species. From this initial list, the limits of our savanna regions were gridded at about 110-km resolution (i.e., approximately 1° resolution) and we spatially filtered species falling within each savanna's grid cell. This resolution has been suggested as the most appropriate working on data of geographic distributions, as it reduces the inclusion of false presences at large spatial scales (Hurlbert and Jetz, 2007). Thus, our final species list represents the reunion of species with distributional ranges that overlap the Cerrado and its proximities.

Functional traits

The functional traits used here represent linear morphological measurements. Thus, the functional variation considered in this study directly relates to morphological aspects. Linear measurements, although they do not geometrically capture the shape of species, have the advantage of being easily recorded, and therefore less prone to sampling errors in multiple source databases such as the one used in this study.

Our functional trait data were obtained from the AVONET database (Tobias et al., 2022). AVONET represents a compilation of individual-level measurements for all extant bird species worldwide aggregated in a standardized manner at the species level. Among the information included in the database are 9 linear morphological traits, including four bill measurements, three wing measurements, tarsus length, and tail length (Figure 2). The choice of morphological characters is based on their established associations with relevant ecological aspects for bird species such as diet, dispersal, and locomotion.

Defining the geographical and functional spaces

The ecomorphological data collected served as the basis for the representation of the functional structure emerging from the bird diversity of Cerrado. First, we segmented the Cerrado in a regular grid composed of cells with 1º x 1º area (hereafter geographical cells). The distributional ranges of species were overlapped with the geographical grid, and the species composition of each cell was registered. Given the morphological values of each species present, an average was taken for all 9 morphological traits. This resulted in a table with the mean values for each trait in each geographical cell.

As recommended, the geographical cell's mean values were scaled to mean zero and standard deviation of one to standardize variation for a principal component analysis (PCA) (Palacio et al., 2022). As a result, a 9 dimensional space was defined based on the Euclidean distances between geographical cells in the functional space. The dimensionality of this space was identified by PCA significance testing using the PCATest package (Camargo, 2022). This test indicates the dimentionaly necessary to describe data variation in the ordination space, identifying only main axes representing the significant functional variation. Ideally for the proposed approach to work, the functional space should be well defined by two dimensions.

With the functional space defined, a functional grid was applied to divide the functional spectrum in each axis by 20 equal intervals. This means that, in a two-dimensional functional space, a regular grid of 400 grid cells (hereafter functional cells) is enough to capture the whole functional variation. For each functional the number of geographical cells, the total area of original native cover and the proportion of native area converted in relation to original cover were registered.

Original native cover and proportion of native area converted

To represent the original native cover and the area of lost native vegetation due to suppressive activities, we used the land cover data from Mapbiomas Collection 8, which details the state and nature of occupation of the Brazilian territory from 1985 to 2022 (Mapbiomas, 2023). We employed the extent of the original data falling within the limits of our geographical grid as a mask to define area values for each geographical cell, calculated by the number of pixels within each cell. Since the Mapbiomas data covers Brazil as a whole, and that cells located at the periphery of the Cerrado expand beyond its limits, we have two situations to pay attention to: i) our native area cover does not only consider areas of Cerrado vegetation; and ii) areas where the Cerrado borders different countries such as Paraguay, part of the cell area will not have data. That's why native area conversion is expressed as a proportion to the original data cover in the cell.

Finally, we created a deforestation mask by combining all anthropogenic land cover classes into a single class representing converted native areas. We then calculated the proportion of native area loss in relation to the original cover for each geographical cell. This calculation indicates the level of occupation for each geographical cell, expressed as the number of converted pixels divided by the original cover.

RESULTS

The cerrado was divided into 255 geographical cells of 1º x 1º (Figure 1A). Two of which, despite having species information, had no baseline data for land cover and were excluded in further analysis. Results below depict the results based on the 253 cells with complete information. Mean values of proportion of native areas converted in Cerrado was 0.50, indicating that on average, 50% of the geographical cell areas are occupied by destructive activities. 132 geographical cells had more than 50% if its native areas were already converted, this means that 52% of Cerrado's geographical cells are under intense environmental degradation (Figure 1B).

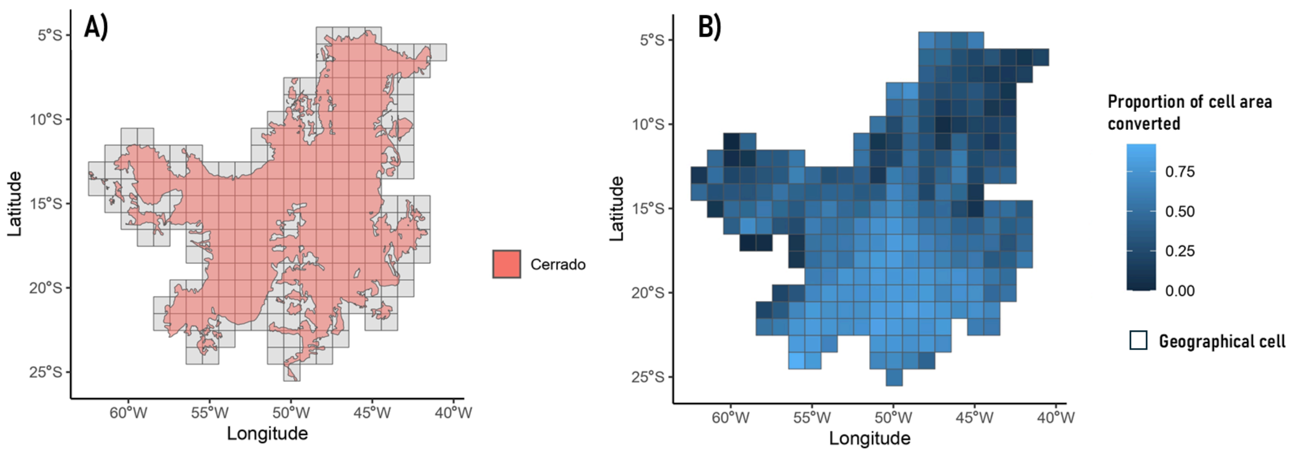

Figure 1. a) Representation of the geographic segmentation of Cerrado by a regular grid of 1 x 1º cells. b) Proportion of cell area converted to anthropogenic land uses. This degradation value is relative to the original native area within the cell. Lighter tones of blue indicate regions with advanced deforestation patterns.

The PCA significance test indicated that the Cerrado's birds functional space represented biologically significant variations with a two-dimensional space composed of PC1 and PC2. This means that the first two components were identified as dimensions significantly associated with systematic sources of variation in the multivariate trait data. The first two PCs explained 81% of the total variation. PC1 (65.7% [CI (95%): 63.5 - 68.1]), and can be interpreted as a size index, with higher PC1 values indicating larger linear measurements of all traits but Hand-Wing index. Meanwhile, PC2 (15.3% [CI (95%): 14.1 - 16.7]) has its variation associated only with the Hand-Wing Index, indicating PC2 as a dimension representative of movement

(Figure 2A).

The functional space defined by the PCA and capturing the spatial variation of Cerrado's birds functional diversity was divided into 400 functional cells of 20 equal intervals. The geographical cells occupied a total of 129 functional cells, indicating that only 32.2% of the functional spectrum was 'realized' (Figure 2B). The number of geographical cells within functional cells varied from 1 to 9, with functional cells on average having approximately two geographical cells in its functional interval (Figure 2B).

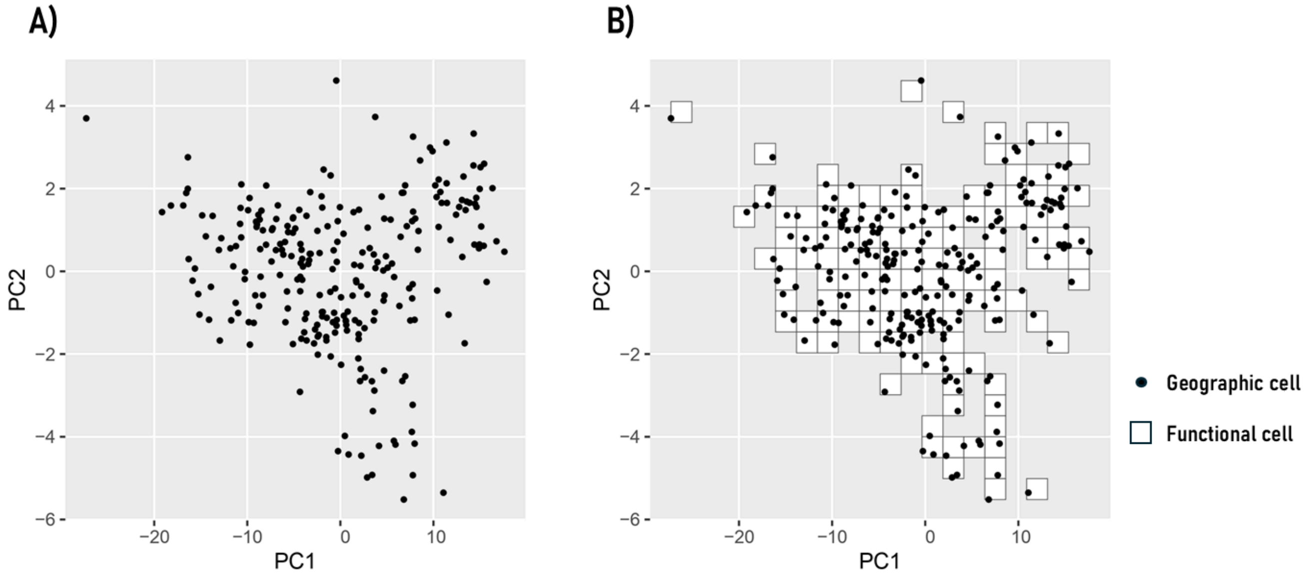

Figure 2. a) Distribution of the 253 geographical cells in the unsegmented functional space. b) Distribution of the same geographical cells in the segmented functional space. Note that some functional cells contain more than one geographical cell.

Values associated with morphological traits are differentially distributed across the Cerrado (Figure 3). PC1 values, mostly related to species overall size, are most notably high in geographical cells where the Cerrado border portions of the Amazon just below 10ºS latitude, and in the northeastern portion where the Cerrado transitions to Caatinga and Atlantic Forest. For PC2 values, related to species Hand-Wing index, lower values are found in the northwestern portion where the Cerrado border the Amazon, indicating a region with species of comparatively lower dispersal abilities.

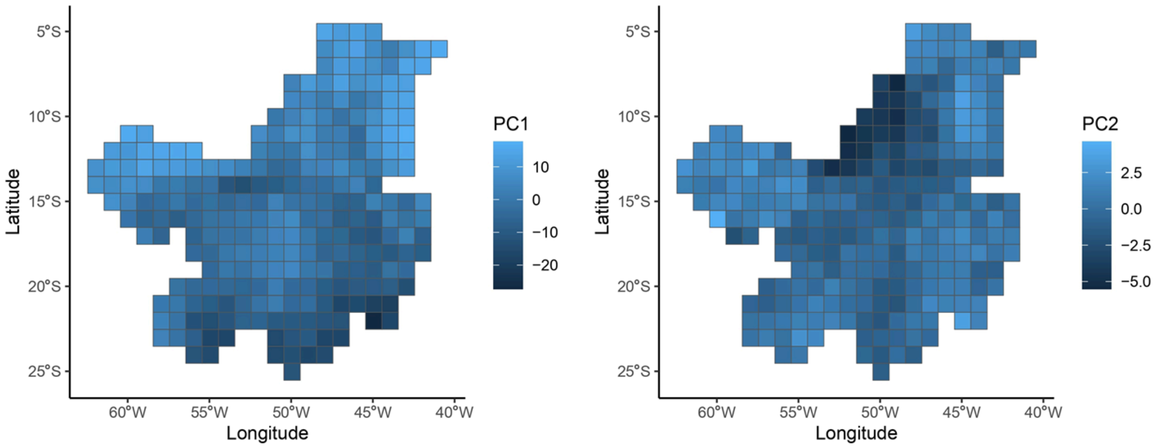

Figure 3. The distribution of PC1 and PC2 values across the geographical cells segmenting the Cerrado. The PC values originate from the PCA made by the average values of the 9 morphological traits in each geographical cell. The lighter tone of blue, larger values of the morphological traits associated with each dimension. Likewise, the darker the tone, lower values of associated traits.

Mapping the geographical information back to the functional space allows us to visualize patterns that more effectively illustrate the functional impact of spatial threats such as habitat loss, on functional diversity (Figure 4). Functional cells with larger geographical areas do not form a contiguous pattern within the functional space, one group appears located in the lower central portion of the spectrum, and another appears located in an upper central portion of the functional space (Figure 4A). Functional cells with larger areas represent trait values that are more 'area protected', while functional cells with lower values represent trait values that are more restricted in the geographical space, and could be potentially more threatened by habitat loss.

When analyzing the functional signature imprinted by the distribution of values of native areas lost to habitat destructive activities, we see a more widespread scenario of erosion across the functional spectrum. Functional cells were on average 52% taken by lost native area. Larger geographical areas only partially buffered functional cells from the pervasiveness of the spatial threats to functional space (Figure 4B). Functional cells with native cover areas larger than the mean had, on average, 51% of their native cover already converted by the year of 2022. This indicates that the effective area of these spatially larger functional cells are considerably reduced. Functional cells of the left portion of the spectrum are more degraded than functional cells of the right portion of the spectrum, indicating a possible erosion starting point for the functional diversity of Cerrado's birds (Figure 4C).

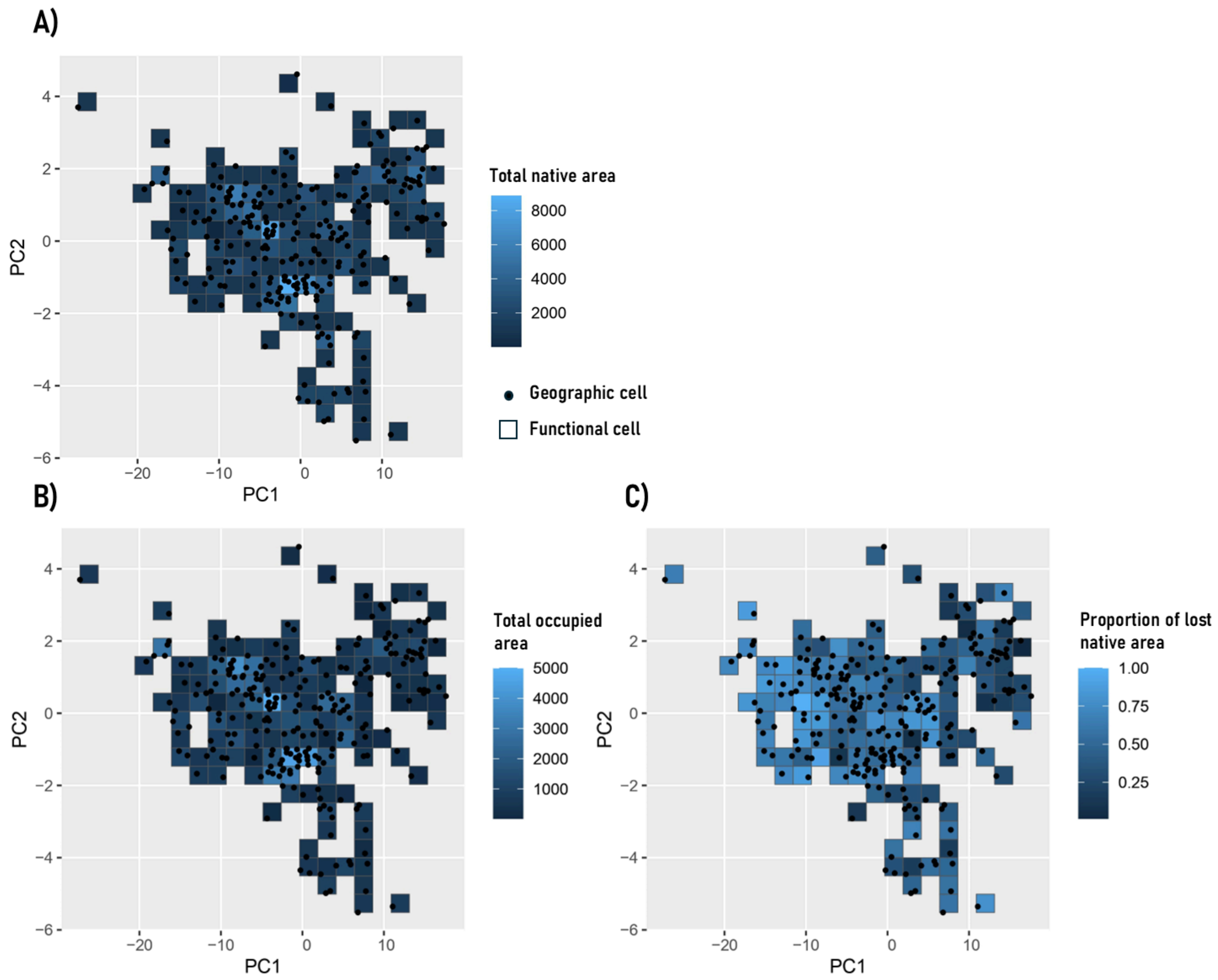

Figure 4. a) The distribution of total native area values in the functional space representing the total original area of Cerrado falling within each functional cell. Note that this variable relates to the number of geographical cells within the functional cell. The lighter the shade of blue, the more original native area there is within the functional cell. Total native area is measured in the number of pixels within cells. b) The values of total anthropogenic occupied areas within functional cells. This value is also related to the amount of geographical cells in each functional cell. The lighter the shade of blue, the more native area devegetation to anthropogenic uses. c) The distribution of the values of proportion of lost native area in the functional space. The lighter the shade of blue, the more advanced is the process of anthropogenic occupation within functional cells, irrespective of functional cell total area.

Reapplying the duality and mapping the functional data back onto the geographical space, we identified specific geographical cells that critically require conservation efforts to mitigate the imminent erosion of the functional diversity of bird species in the Cerrado biome (Figure 5). In particular, we found 34 geographical locations falling within 21 functional cells that are experiencing advanced stages of native habitat loss, with a proportional native area loss of 75% or more.

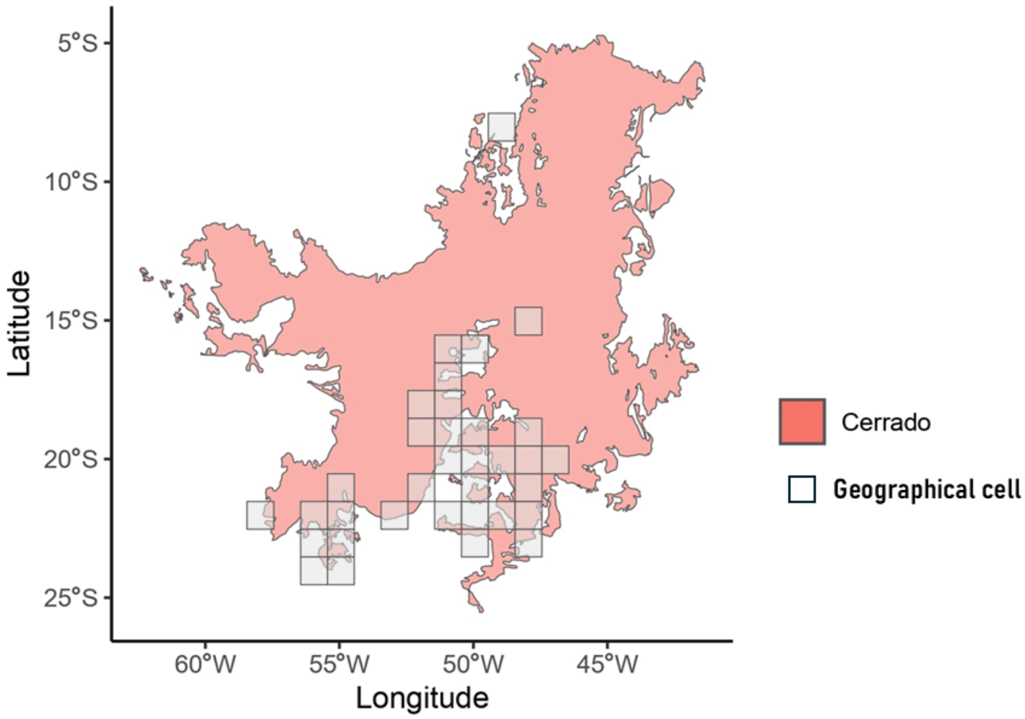

Figure 5. Location of the 34 geographical cells belonging to the 21 functional cells with advanced stages of native area occupation (Proportional of lost native area > 75%).

DISCUSSION

In this study, adapting Coelho et al. (2023) conceptualization of geography of climate, we applied Hutchinson's duality reasoning to map the spatial distribution of Cerrado's birds morphological variability in the functional space. Much of the functional diversity science has focused on the functional impact of species loss looking at the overall structure of the functional spectrum. Despite the ecological and evolutionary importance of functional structure conservation, this approach gives little direction for conservation planning actions much needed to avoid extinctions. Our study demonstrates how the functional diversity analysis framework can be applied to spatially guide trait diversity conservation over large spatial scales.

We showed that only 32.2% of the functional spectrum is currently occupied by the Cerrado bird diversity, and that some realized functional regions, based on their total area, are more geographically representative than others. This implies that trait value combinations have distinct geographical signatures. This functional expression on the geographical space suggests that the functional spectrum is also under different levels of impact caused by spatial threats such as habitat loss, as it was observed for the studied functional space of Cerrado.

Reflecting the advanced consolidation state of habitat destructive activities in the Cerrado (Buchadas et al. 2022; Machado and Aguiar, 2023), many functional regions presented devegetation indices of approximately half of their total area. Since functional cells contain different numbers of geographical cells, some trait combinations are more "spatially insured" than others. However, even larger functional cells presented high levels of anthropogenic occupation, indicating that the functional impact of human activities on bird diversity in the Cerrado is pervasive. One of the consequences of the land use pattern of the Cerrado is the homogenization of landscapes (Mapbiomas, 2023). Land-use diversity has been identified as a predictor of taxonomical and functional diversity for birds globally (Martínez-Núñez et al. 2023). Given the land use state of the studied neotropical savanna, it is clear that the process of diversity loss is already widespread, and could potentially be aggravated by future environmental changes (Hidasi-Neto et al. 2022).

Our results highlight opportunities for trait diversity conservation by identifying the most likely starting portions of a functional erosion process caused by habitat loss in the Cerrado and pinpointing the respective geographical regions where intervention is needed to mitigate it. These regions are primarily located in the southern Cerrado, where historical anthropogenic activities first took place, resulting in highly fragmented landscapes (Lapola et al. 2014; Aguiar et al. 2016). In a large-scale conservation strategy aimed at preserving the functional trait diversity of savanna birds, prioritizing these critical geographical cells is crucial. This emphasizes the value of trait-based scientific knowledge in guiding systematic conservation planning and environmental management to protect biodiversity and their associated ecosystem functions.

The value of Hutchinson's duality in the studies of functional diversity conservation lies in its broad applicability. The premise is that with its reasoning, one can study the geographical signatures on multidimensional spaces and multidimensional signatures in the geographical space. This makes it an important analytical tool for studies of functional diversity of many conservational goals and scales. Here we apply Hucthinsoon's duality considering a multidimensional space built by axes of continuous variation (i.e. morphological data), but categorical data can also be incorporated in our approach by applying the appropriate ordination method for each case (Bello et al. 2020). Categorical traits themselves may represent a combination of many functional traits values, but can be used to a more ecologically defined ordination of species in the functional spectrum. Traits can also be selected based on their "response" or "effect" characteristics (Diaz et al. 2013; Hordley et al. 2021). In any case, for interpretability and applicability, transparency regarding decisions of functional traits and analytical procedures are important (Palacio et al. 2022).

Our use of bird functional data was grounded in well-established trait definitions and on the advanced stage of functional data systematization for this taxa (Tobias et al. 2022). We also relied on the demonstrated statistical relationship between morphology and ecological function in bird species (Pigot et al. 2020). We propose that our method can be extended to other groups, such as invertebrates and plants (Saatkamp et al. 2018; Bucholtz and Egerer, 2020), to guide conservation actions aimed at restoring biodiversity and associated functions (Carlucci et al. 2020). Incorporating other types of spatial data can provide more detailed assessments of the functional impacts of geographical threats or other spatial manifestations. Future studies could integrate multiple scales and taxa to enhance the scope of such analyses. Model statistics can also be employed to identify data patterns, assess the potential for generalizing results, and applicability in predictive studies. This would test the limits of Hutchinson's duality in informing systematic conservation planning focused on protecting functional diversity and its associated ecosystem functions and services.

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CONSIDERAÇÕES FINAIS

Esta tese investigou a diversidade funcional de savanas tropicais, através de análises focadas em sua manifestação no espaço funcional. Ao longo de três capítulos, a tese demonstra como a estrutura funcional emergente dos conjuntos regionais de espécies oferece insights relevantes para a conservação. No primeiro capítulo, analisamos detalhadamente as estruturas funcionais das espécies do Cerrado, das Savanas Africanas e da Austrália. Os resultados indicam que as savanas tropicais possuem alta riqueza e redundância funcional, e que as métricas taxonômicas não capturam plenamente a magnitude do componente funcional da diversidade de aves nessas regiões. Identificamos que, mesmo dentro de um espaço funcional amplamente compartilhado, as espécies estão organizadas geograficamente e ecologicamente em regiões funcionais associadas a nichos tróficos específicos. Cada nicho apresentou uma assinatura funcional distinta, o que reflete a multiplicidade de contribuições da diversidade na formação dessas estruturas funcionais. Esses achados reforçam o potencial de se considerar aspectos estruturais da diversidade funcional como possíveis indicadores da integridade ecológica em ações de conservação em diferentes escalas.

Essa compreensão dos espaços funcionais e sua importância para o planejamento da conservação foi aprofundada nos capítulos dois e três. No segundo capítulo, investigamos a distribuição espacial da diversidade funcional das aves do Cerrado e os possíveis impactos funcionais de ameaças como a perda de habitat. Descobrimos que as características que definem a diversidade funcional estão distribuídas de forma desigual ao longo do Cerrado, refletindo diferentes níveis de vulnerabilidade. Ao examinar a interação espacial entre atributos funcionais e perda de habitat, conseguimos identificar regiões prioritárias para conservação, seja por meio de restauração ou proteção, destacando a importância de um planejamento espacial eficaz para uma preservação global da diversidade funcional das aves no Cerrado.

No terceiro capítulo, expandimos a abordagem da conservação da diversidade funcional, aplicando o conceito de Dualidade de Hutchinson para mapear a distribuição espacial da variabilidade funcional das aves do Cerrado. Grande parte dos estudos de diversidade funcional foca no impacto da perda de espécies e suas consequências na estrutura global do espectro funcional. Embora essa abordagem seja importante, ela oferece pouca orientação para o planejamento de ações de conservação que possam evitar essas perdas. A estrutura funcional começa a ser degradada muito antes da extinção total das espécies. Neste capítulo, aplicamos a dualidade de Hutchinson, que estipula uma relação recíproca entre o espaço do nicho e o espaço geográfico, para mapear os impactos potenciais de ameaças geográficas no espaço funcional. Essa abordagem nos permitiu identificar combinações funcionais que estão mais "espacialmente asseguradas" e outras mais ameaçadas. Também identificamos uma possível direção de erosão do espaço funcional das aves do Cerrado, bem como áreas geográficas onde intervenções são necessárias para mitigar essa perda de diversidade funcional.

As abordagens utilizadas nesta tese podem ser adaptadas a outros grupos taxonômicos, em escalas mais detalhadas e para diferentes manifestações espaciais (como invasão de espécies, regimes de perturbação ou extremos de temperatura), além de serem complementadas por outras abordagens ecológicas, como redes ecológicas (abordagem ecológica também muito focada no estudo dos processos ecológicos emergentes de padrões estruturais). Nosso principal objetivo foi demonstrar o potencial da análise detalhada da dimensão funcional da diversidade para estudos de conservação. As análises de impactos antrópicos na biodiversidade ainda se concentram principalmente em aspectos taxonômicos, ignorando dimensões da diversidade que podem estar sustentando a aparência e funcionamento dos sistemas naturais, mesmo que de maneira frágil. É necessário desenvolver técnicas que nos permitam antecipar os impactos funcionais antes da extinção das espécies. Embora experimentos sejam fundamentais para gerar esse tipo de informação, eles enfrentam limitações em termos de escala ecológica e espacial. Estudos futuros podem investigar, de forma empírica, o significado ecológico das características estruturais da diversidade funcional e seu papel na conservação da biodiversidade e dos serviços ecossistêmicos associados.

Finalmente, os estudos realizados nesta tese foram viabilizados pela existência de um banco de dados público que reúne informações morfológicas de todas as espécies de aves registradas. Esse tipo de sistematização de dados biológicos é fruto de um investimento histórico em pesquisa básica, que fornece os blocos essenciais para a construção de conhecimento que permitem avanços disciplinares. Esforços para sistematizar dados funcionais de outros grupos taxonômicos estão em andamento, mas é crucial que mais investimento e atenção sejam dedicados a esse tipo de trabalho científico para que análises como as propostas nesta tese possam ser facilmente estendidas para múltiplos grupos taxonômicos e para o planeta.