

João Paulo dos Santos Vieira de Alencar

**Síntese, regionalização e determinação de
áreas prioritárias à conservação de
tetrapodas endêmicos da savana mais rica e
ameaçada do planeta - o Cerrado**

*Synthesis, regionalization, and priority areas for the conservation
of endemic tetrapods in the richest and most threatened savanna
on the planet - the Cerrado*

São Paulo - SP

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Versão corrigida

Tese apresentada ao Instituto de Biociências da Universidade de São Paulo como parte dos requisitos para obtenção do título de Doutor em Ciências, na área de Ecologia de Ecossistemas Terrestres e Aquáticos

Universidade de São Paulo

Orientador: Cristiano de Campos Nogueira

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São Paulo - SP
2023

À dona Inocência, dona
Sansão, dona Antônia,
dona Neuza, dona Marina,
dona Cacilde e Bea

“[...] Thus, while investigators may search for satisfying, simplistic explanations for the origins of endemics, what they often find is a complex picture, explained in part by Earth history and in part by past and present ecological processes - sometimes confounded in ways that are hard to disentangle, although our ability to do so is getting better all the time.”

(Alfred Russel Wallace, 1876)

*“[...] Ei irmão nunca se esqueça, na guarda, guerreiro
Levanta a cabeça truta, onde estiver seja lá como for
Tenha fé porque até no lixão nasce flor.”*

(Pedro Paulo Soares Pereira - Mano Brown, 1994)

*“[...] Meto terno por diversão
É subalterno ou subversão?
Tudo era inferno, eu fiz inversão
A meta é o eterno, a imensidão
Como abelha se acumula sob a telha
Eu pastoreio a negra ovelha que vagou dispersa
Polinização pauta a conversa
Até que nos chamem de colonização reversa.”*

(Leandro Roque de Oliveira - Emicida, Jé Santiago e Rui, 2019)

Agradecimentos

Como todo trabalho complexo que tem algum êxito em suas metas e objetivos, essa tese foi escrita à varias mãos (e mentes). É um trabalho árduo conseguir contemplar todas as pessoas que participaram passiva ou ativamente da produção dessa tese, especialmente por que algumas pessoas podem ter contribuído de formas tão singelas, como com um “Bom dia” e um sorriso aberto cheio de simpatia ou com um cuidadoso “Moço, você esqueceu o guarda-chuva”, que a gente, na correria do dia-a-dia acaba não contabilizando. Olha... de fato, eu fui escrevendo até lá embaixo e voltei aqui com a conclusão de que: não dá pra incluir todo mundo da forma que me agradaria. De todo modo, algumas pessoas foram decisivas e marcaram com força esse trabalho, das quais, quero destacar:

Para começar pelo essencial e sem o qual eu jamais teria sequer estar aqui hoje, eu gostaria de agradecer à minha família. Dona Neuza e Ana Beatriz (Bea) você são uma fonte constante de inspiração e motivação pra seguir. É olhando para o quanto vocês já fizeram por mim, seja literalmente investido na minha educação, ou apenas aceitando um abraço e um beijo “do nada” no meio do dia, que eu percebo que chegar até aqui seria impossível sem vocês na minha vida. À dona Antônia, que não vai ler isso por que a vida foi dura e exigiu mais da mãe de dez filhos do que o processo de alfabetização poderia oferecer no momento, mas que sei que esse agradecimento vai lhe chegar, meu muito obrigado! Não apenas por ser a matriarca dessa família e por ter dado condições de tanta gente estar aqui e fazer parte desse conjunto de pessoas tão diversas e quase sempre queridas, mas por ter a paciência de me contar, recontar e contar de novo TODAS as vezes que eu lhe perguntava sobre nossos ancestrais de que a senhora tem lembrança. Foi um prazer, e um presente sem tamanho conhecer através da senhora, um pouco sobre dona Inocência, escravizada, cuja filha “escapou do tronco por nascer branca” (e se tornou minha tataravó, dona Joana), e sobre dona Sansão, indígena, “pega no laço enquanto estava caçando calango no sertão da Bahia”. Obrigado!

Sr. Paulo Sérgio, Gui, João Vitor e Aninha, mesmo dada a distância, nossos encontros esporádicos sempre estiveram abertos para acontecer e eu sou feliz com vocês todas as vezes que eu os encontro. Que possamos viver cada vez mais momentos tão prazerosos com os que temos juntos.

Se eu usasse esse espaço para agradecer adequadamente cada uma das pessoas que eu gostaria, eu precisaria de quase o dobro de páginas nessa tese. Então, embora eu certamente não agradeça como vocês merecem de fato, gostaria de deixar registrado meu muito obrigado à: Letícia Arruda, Isa, Clatinha e Lá, que dividiram um pouco de suas vidas comigo durante a pandemia, dando risada de Greg News e formando os melhores squads de Free Fire nas horas vagas. Lê, que me acompanhou em boa parte dessa trajetória, com altos e baixos e que com frequência esteve aqui pra me acolher em alguns momentos, que

teve e me deu espaço pra compartilhar planos e frustrações, obrigado! De Três Lagoas-MS e Rio Claro-SP: Marina, Naka, Erison, Lara, Samuli, que de um jeito ou de outro estiveram presentes, mas sempre proporcionando momentos de alegria de descontração, obrigado! Da Eco: Carol, Eletra, Richie, Isabela, Mila, Bruno, Pamela, Pam, Soly, John, Érika, Andrés, Lucas Freitas, Lucas Camacho, Lucas Taio, Mena, Amanda, Jennifer, Joyce, Marianela, Lari, Juliete, Coxinha, Morés, Doug, Arthurito, Dieguito, Jonathan, Gabriel, Caetano... Uff... É impossível seguir com essa lista e não deixar nenhum nome para trás, por isso mencionei principalmente a galera que esteve comigo nesse último ano, pós retorno presencial ao departamento. Mas, entre as pessoas do pré-cambriano: Rodolfo Pellison, Bruna tutz, Dani Coelho, Isa Romitelli, Julia Barreto, Duda, João (G-sus), Adrian, Chico, etc... etc... Desculpa gente, é difícil rs tenho MUITOS mais colegas do PPG-Eco que compartilharam café, breja, bandejão, rolê, preocupação com comitê, com qual, com tanta coisa... Se seu nome não apareceu aqui e você sentiu falta disso, saiba que não foi por falta de vontade ou de reconhecimento. De todo modo, o final desse parágrafo dos agradecimentos vai a toda comunidade discente do PPG-Eco, que com maior ou menor proximidade fez desses anos um dos períodos mais relevantes da minha vida. Meu muito honesto, obrigado!

Iniciando o lado acadêmico dos agradecimentos gostaria de começar por meu orientador, Dr. Cristiano de Campos Nogueira, CriNog ou só CN quando a mensagem era pra ser ligeira. CriNog, obrigado por me acolher como seu aluno para uma jornada tão brilhante quanto a que foi desvendar um pouquinho e aprender tanto sobre o que é, na teoria e na prática o nosso Cerrado. Foi graças a sua paixão e dedicação em fazer o melhor possível com o que temos em mãos que eu abri o coração e deixei o Cerrado dominar meus interesses de forma tão significativa ($p < 0.0001$, risos). Obrigado por caminhar, lado-a-lado nesse trajeto e por usar de forma sábia e respeitosa toda a experiência a mais que tem sobre essa maravilha que é o Cerrado, suas espécies endêmicas, a vida acadêmica e seus percalsos e a vida como um todo.

Ao chefe, Professor Dr. Marcio Martins, que desde o dia da minha entrevista com o CriNog já cedeu um espacinho pra eu usar no LabVert, que se tornou minha “segunda casa” em muitos aspectos, entre eles, o de me sentir bem lá dentro. Agradeço por todas as oportunidades que me deu de ir a campo, com e pelo laboratório, foi assim que eu pela primeira vez entrei em contato de fato com algumas das espécies que eu viria a estudar e conhecer melhor nessa tese.

A mi jefe en el exterior, Javier Nori, quien me recibió con los brazos abiertos con el desafío de guiarme en el desarrollo de uno de los capítulos de mi tesis, y quien con tanto éxito y eficiencia contribuyó a la primera publicación resultante de esta tesis. Javi, las lecciones que aprendí de Córdoba van más allá de lo que necesitaría para terminar esta tesis o publicar un artículo. Ya les he dado las gracias muchas veces, personalmente, por correo electrónico, por WhatsApp, y creo que todavía no he podido expresar adecuadamente

mi gratitud por haberme ayudado a mantener la llama encendida y a seguir invirtiendo en mi carrera científica. ¡Muchas gracias!

Ao meu comitê de acompanhamento, Ana Paula Carmignotto, Luis Fábio Silveira, Paula Hanna Valdujo e Ricardo Jannini Sawaya. Obrigado por comprarem essa jornada com a gente e por bancarem a loucura de fazer mais reuniões do que “deviam”. Todas as conversas, em grupo ou individuais, foram fundamentais. Paulinhas e Luis Fabio, super obrigado pela paciência e disponibilidade de tempo para rever comigo quais espécies dos grupos de especialidade de vocês deveriam ou não entrar nas análises. Ricardo, cara, obrigado pela assertividade constante em todas as reuniões. Com vocês foi possível voar, mas sem perder o chão de vista. Obrigado!

Agora, falando um pouco mais de colaborações, mas da galera que esteve mais próxima, lado-a-lado, desde o começo. Em primeiro lugar, não posso deixar de mencionar Bruna Espinosa Bolochio. Bru, você foi a primeira pessoa que, pacientemente, sentou comigo e abriu um *script* no R. Na época, a ideia era pra aprender, por cima, como desenrolar a análise de Elementos Bióticos (usada no capítulo 2). Mal sabia que eu nunca tinha nem visto a interface desse programa antes (risos). Além disso, você foi minha principal fonte personificada de inspiração para ir para Córdoba para conhecer e trabalhar com o Javier. E que baita experiência isso me proporcionou! *Chica, muchas gracias*, por ser essa pessoa tão disposta (mais ou menos), e que, acredite ou não, fez toda diferença pra essa tese ter um ponta-pé inicial.

Ainda nessa vibe, agradeço a meus e minhas colegas de laboratório. Seja pelas conversas esporádicas, viagens de campo, cafezitos, brejas, discussões sérias sobre alguns temas, acadêmicos ou não, ou pela colaboração direta para publicação de alguns trabalhos. No grupo galera de campo, teria que agradecer meio mundo aqui (risos), mas deixarei pra agradecer quem me estimulou, de certo modo, a conhecer algo pra além da minha zona de conforto (se é que existe isso na vida acadêmica ou de biólogues de campo), aqui Gabriella Neves Leal Santos e Rosana Campos Paschoalino. Gabi e Ro, obrigado pelo tempo que me proporcionaram em Monte Verde caçando *Lachesis* no cupinzeiro, me atuar reclamando de frio e pechinchando preço de queijo em Camanducaia. Nesse grupo de colaboradores em publicações, agradeço em especial: Juan Camilo Díaz Ricaurte(R), Filipe Alexandre Cabreirinha Serrano, Giovanna Ribeiro Felicio e Luciana O. Furtado. Obrigado pela confiança na minha colaboração, pelas ideias e pela parceria.

A experiência de qualquer pessoa que passar pelo PPG-Eco nunca será completa se essa pessoa não passar por pelo menos duas das comissões de organização e representatividade discente que existem no programa. Fui felizardo de participar de quase todas, e mais um pouco hahaha. Entre as principais, Comissão PROEX, EcoEncontros, EcoEscola e Café Existencial (que não tem comissão, mas tem - aparentemente ainda em crise com a própria existência), foram alguns dos espaços mais importantes de aprendizado e trocas de ideias no programa. Apesar de serem de participação facultativa, são essenciais para

que a passagem pelo PPG-Eco seja ainda mais potente. Obrigado!

Ainda entre as “comissões”, gostaria de deixar um agradecimento especial ao Coletivo Bitita, o coletivo negro do Instituto de Biociências da USP. O coletivo nomeado em homenagem à Maria Carolina de Jesus (Bitita) me ampliou a perspectiva do que mais faltava eu entender sobre meu lugar na USP, que embora tenha sido um lugar de privilégio, é também um lugar de resistência e que demanda luta, organizada e bem estruturada pra avançar em direção a um mundo mais justo, inclusivo e bonito de se viver.

E falando em luta, gostaria de agradecer imensamente à Bruna de França Gomes e a Luís Felipe Natálio por formarem comigo a primeira chapa tripla de Representação Discente no PPG-Eco. Ter vocês ao meu lado nessa empreitada for um dos acontecimentos que mais me fez acreditar que sim, as vezes a gente tem a sorte de cruzar com as pessoas certas na hora certa e que isso faz uma diferença danada na nossa vida. Obrigado!

Desde a primeira semana inaugural que passei no PPG-Eco o padrão já era claro... Vera, a pessoa mais constante nos agradecimentos de teses e dissertações. Seria simplesmente impossível não começar essa parte de agradecimentos ao quadro de funcionários da USP sem começar por você Verinha. Quase sempre disponível e sempre disposta a nos ajudar a entender das questões burocráticas do programa, do departamento, do instituto e da USP. E olha que não foram poucas a vezes que precisei tentar entender alguma dessas coisas e você prontamente me salvou. Tô escrevendo isso aqui e já pensando que daqui a pouco irei à sua sala pra avançar com o processo de depósito e outras coisas, então achei válido deixar registrado esse agradecimento por algo que ainda vai acontecer no futuro, sem deixar de reconhecer todas as vezes que já esteve presente por mim e por colegas no passado, e com a garantia que sua presença no PPG-Eco marcou a minha história pra sempre. Um beijo Verinha!

A todo o corpo técnico fixo, em especial Luís, Wellington, Melina e Shirlene, e aos funcionários terceirizados que passaram pelo IB. Obrigado!

A todas e todos os docentes que cruzaram meu caminho oferecendo disciplinas durante a pós-graduação na Ecologia da USP: Adriana Martini (Dri), Alexandre Adalardo de Oliveira (Alê), Beny Spira, Bruno Travassos de Britto, Camila Castanho, Cristiano Nogueira (CriNog), Cristina Yumi Miyaki, Gabriel Nakamura (Naka), Glauco Machado, Eduardo Santos (Edu), Marcio Martins, Marco Mello e Maria Cristina Arias. Obrigado pela dedicação de vocês, pela paciência em tirar tantas dúvidas e mediar tantas discussões produtivas em sala de aula (ou remotamente). Todas as disciplinas que fiz com vocês foram enriquecedoras e sem dúvida contribuíram para que eu chegassem até aqui confiante de que tenho conhecimento teórico e técnico para encarar desafios cada vez maiores pela frente. Obrigado.

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jamentos e roteiros de aula e pude presenciar em primeira mão os olhares entusiasmados dos alunos e alunas quando percebiam que estava aprendendo algo novo e intrigante. Reconheci que a docência é um caminho tortuoso, mas com pequenas recompensas ao longo do trajeto que fazem com que a gente siga motivado(a).

Ainda falando sobre o corpo docente do PPG-Eco, gostaria de agradecer pela experiência única proporcionada pelas professoras e professores que compuseram a Comissão de Coordenação do Programa (CCP) durante minha passagem pela Eco, e mais especificamente no período que eu fui presenteado com a função de representar o corpo discente do programa. A representação discente foi um dos desafios mais marcantes da minha trajetória pelo PPG-Eco. “Começo” de pandemia, tudo ainda sendo ajustado para o formato remoto, e o início de um distanciamento extremamente doloroso e custoso para mim, meus colegas e para o programa. O que chegou até mim como uma “bucha”, em pouco tempo, naquele momento específico, se transformou e se tornou meu maior propósito como discente. Para muito além de produzir uma tese, escrever artigos e afins, eu me vi num espaço potente de aprendizado e transformação. Discutir a reserva de vagas para grupos sub-representados na pós-graduação? Discutir quanto mais o corpo discente precisa de grana pra resolver seus B.Os acadêmicos?? Recesso??? Eram coisas que eu jamais imaginei que teriam sequer abertura para discussão, ainda mais em um dos lugares mais brancos, elitistas e tradicionais, da academia latino-americana. E que surpresa agradável eu tive ao me deparar com uma comissão coordenadora tão dedicada e preocupada em cuidar de seu corpo discente. Poderia passar mais algumas horas aqui matutando o tanto que essa experiência foi marcante, mas preciso mesmo fechar esses agradecimentos e correr pra depositar essa tese ainda hoje. Assim, queria apenas destacar três nomes, Paulo Inácio, Renata Pardini e Alê. Para além de agradecer vocês por serem as pessoas maravilhosas que são, eu achei mais importante dizer algo que me deixa mais feliz e emocionado de ter conhecido e participado de discussões com vocês: Vocês me dão esperança! E esperançar foi uma das coisas mais gostosas que eu pude experimentar no PPG-Eco.

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Prefácio

Fazer ciência, se feito da maneira correta, deveria despertar e estimular reflexões que vão para além do meio acadêmico. E assim o foi, para mim. Eu depositei essa tese na esperança de que, de alguma forma, o conhecimento aqui produzido seja aproveitado. Seja para o avanço das ciências da biogeografia e conservação; seja para destacar um pouco mais a riqueza e exuberância do Cerrado, a “maior, mais diversa e mais ameaçada savana tropical do planeta” como lerão repetidas vezes mais adiante; ou apenas para estimular futuros e futuras pesquisadoras mostrando que mesmo no grau mais elevado de formação acadêmica nós cometemos erros, nos equivocamos e precisamos, reler, refletir, parar, para ai então avançar. Me peguei, nesse momento, pensando que talvez em algum momento eu voltarei para reler isso que estou escrevendo agora e pensarei no quanto eu poderia ter melhorado esse texto, apesar de nem ser obrigatório. Mas lembrei também do quanto foi difícil finalizar os detalhes desse documento em pleno feriado prolongado do dia do trabalhor, e assim vou me desculpar por não ter caprichado tanto assim (nessa parte), e espero que vocês também possam me desculpar.

Me desculpem também por entregar uma tese, que por si só já tem tanta complexidade, com os textos dos principais capítulos em inglês, o que sei que é uma potencial barreira de compreensão para algumas pessoas. Partir com os esboços iniciais já em inglês me ajudou bastante a concluir essas versões e me garante que pelo menos o passo de tradução pós-defesa poderá ser dispensado, o que não quer dizer que o passo de “revisão por *native speaker*” deixará de existir (risos). Tirando que decidi reunir todas as referências apenas no final do documento, os capítulos são apresentados em formato de artigo, supostamente “prontos para submeter”. Na verdade, dois deles já foram submetidos e, felizmente, um já está aceito e em processo de editoração para publicação (iháá). Eu claramente só consegui isso por ter comprado as dificuldades de escrevê-los em idioma estrangeiro. Esse formato ajuda bastante a praticar desde já a concisão e clareza, mas nos limita a uma “conversa” mais “quadrada” com o(a) leitor(a), e além disso, vão perceber que embora a ideia de concisão seja alcançada nos capítulos individualmente, para a tese como um todo algumas coisas ficaram repetitivas. Isso aconteceu por que pra cada artigo nós precisamos explicar detalhadamente algumas coisas que são em comum nos três, por exemplo, a área de estudo e a origem e obtenção da base de dados. Mais uma vez a justificativa é a de que queria adiantar bem o lado para que as publicações saiam rapidinho (“a esperança é a última que morre”, não é mesmo?). Tomara que isso não aborreça muito a leitura de vocês.

Mas, “Calma! calma! Não criemos pânico!”. Aqui na tese eu também escrevi um resumo, introdução e conclusões gerais em português! Busquei deixar a escrita nesses tópicos o mais completa e mais leve possível para que você possa escolher entre conhecer

apenas o contexto geral e principais conclusões do trabalho ou entre mergulhar com de cabeça nas questões mais técnicas e específicas de cada capítulo (escolha não aplicável à banca, sinto muito - risos). Bem... aproveitei esse espaço pra quebrar um pouco o gelo e dar um pouco de respiro do formato quadradão que virá a seguir. Espero que, à quem se aventurar a ler bastante da tese, a leitura seja leve e proveitosa, apesar das mensagens preocupantes que temos que passar adiante. Boa leitura!

Resumo

VIEIRA-ALENCAR, J. P. S. (2023) **Síntese, regionalização e determinação de áreas prioritárias à conservação de tetrapodas endêmicos da savana mais rica e ameaçada do planeta - o Cerrado.** Tese de Doutorado - Instituto de Biociências, Universidade de São Paulo, São Paulo.

A biogeografia procura explicar a distribuição das espécies, e/ou taxa mais elevados, no espaço geográfico. As distribuições geográficas das espécies podem ser limitadas por fatores históricos, ligados à história da terra e da dinâmica ambiental das áreas que habitam, e/ou ecológicos, ligados a fatores intrínsecos da espécie e das espécies com as quais interage. Detectar padrões gerais de distribuição da diversidade contribui para a discussão sobre os papéis de fatores históricos e geológicos na geração de biotas, e também aprimora o processo de tomada de decisão para fins de conservação. No entanto, os padrões de distribuição detectados em escalas locais, mais refinadas, são escassos e muitas vezes referentes apenas a alguns grupos bem estudados (por exemplo, aves e mamíferos). O Cerrado é a maior e mais diversa savana neotropical. É composto por uma diversidade de fisionomias que proporciona alta heterogeneidade ambiental, variando de extensos campos de gramíneas a formações florestais. Essa diversidade de ambientes levou à diversificação faunística com elevada seleção de habitat, gerando formas especialistas nas diversas fisionomias mais predominantes. Desse modo, o Cerrado é marcado por elevado nível de endemismo, já reconhecido anteriormente para plantas, e mais recentemente para vertebrados. No entanto, mais de 55% de sua extensão territorial foi convertida a usos antrópicos, formando mosaicos potencialmente inhabitáveis para muitas espécies, especialmente as de distribuições geográficas mais restritas ou mais exigentes em qualidade de habitat. Essa combinação de elevadas taxas de endemismo e acelerada taxa de conversão de habitats naturais para fins antrópicos rendeu ao Cerrado o título de “*Hotspot* de conservação da biodiversidade”, que parte da estratégia de detectar regiões do globo que são altamente “insubstituíveis”, por conter alto número de espécies exclusivas, e altamente vulneráveis devido à alta perda de habitats. Não obstante, menos de 11% da extensão territorial do Cerrado está atualmente sob proteção legal, dos quais menos de 3% são unidades de conservação de proteção integral. Além de representar apenas uma pequena proporção da extensão do Cerrado, as áreas protegidas existentes não estão distribuídas uniformemente em todo o seu território. Nessa tese nós compilamos e avaliamos 13.800 registros únicos relacionados à distribuição geográfica de 340 espécies de vertebrados terrestres endêmicos do Cerrado sob prismas de biogeografia histórica e biogeografia da conservação. No primeiro capítulo, avaliamos o aumento do número de espécies endêmicas do Cerrado nos últimos anos (2000-2020) e exploramos padrões biogeográficos geralmente associados a espécies de distribuição restrita em detrimento do avanço acelerado de diferentes usos do solo sobre habitats naturais.

Nesse capítulo destacamos que o ritmo acelerado de descrição de novas espécies de vertebrados terrestres endêmicos do Cerrado não é acompanhado por esforços de conservação, e destacamos limitações associadas à avaliação do risco de extinção dessas espécies, majoritariamente para espécies de distribuição mais restrita, descritas recentemente. No segundo capítulo apresentamos uma proposta de regionalização em que detectamos 29 regiões com grupos de espécies co-distribuídas não aleatoriamente, formando bases para discussões sobre a origem e evolução dessas biotas exclusivas do Cerrado. Os resultados foram discutidos em comparação com padrões anteriormente detectados com dados de distribuição de anfíbios e répteis Squamata, e revelam possível generalização do padrão detectado para diferentes grupos de vertebrados terrestres. Por fim no terceiro capítulo trazemos uma proposta de áreas prioritárias para a conservação das espécies analisadas, e discutimos o efeito das mudanças no uso do solo entre 1985 e 2020 sobre a detecção de áreas prioritárias à conservação da fauna de vertebrados endêmicos dessa savana que é a mais rica e ameaçada do planeta.

Palavras-chaves: Cerrado, Endemismo, Regionalização, Conservação, Hotspot.

Abstract

VIEIRA-ALENCAR, J. P. S. (2023) **Synthesis, regionalization, and priority areas for the conservation of endemic tetrapods in the richest and most threatened savanna on the planet - the Cerrado.** Doctoral Thesis - Instituto de Biociências, Universidade de São Paulo, São Paulo.

Biogeography is the study of the distribution of species and higher taxa within geographical space. The distribution of species can be affected by historical factors, such as the Earth's history and environmental dynamics within their habitats, as well as ecological factors, such as intrinsic characteristics of the species and their interactions with other species. Detecting patterns of diversity distribution can shed light on the roles of historical and geological factors in generating biotas and aid in decision-making for conservation efforts. However, local scale distribution patterns are often limited and primarily focused on well-studied groups, such as birds and mammals. The Cerrado, the largest and most diverse neotropical savanna, comprises a variety of physiognomies that provide high environmental heterogeneity, ranging from grasslands to forest formations. This environmental diversity has led to faunal diversification and specialization in the various predominant physiognomies, resulting in a high level of endemism for both plant and vertebrate species. Unfortunately, over 50% of the Cerrado's territorial extent has been converted to anthropic uses, forming potentially uninhabitable mosaics for many species, particularly those with more restricted geographical distributions or higher habitat quality requirements. The Cerrado is therefore designated a "biodiversity conservation hotspot", reflecting its high number of unique species and vulnerability due to habitat loss. Despite this, less than 11% of the Cerrado's territorial extent is currently under legal protection which less than 3% being strict protection reserves. Moreover, besides the poor extension coverage, existing protected areas are not evenly distributed throughout its territory. This thesis compiles and evaluates 13,800 unique records related to the geographical distribution of 340 endemic terrestrial vertebrate species in the Cerrado from the perspectives of historical biogeography and conservation biogeography. The first chapter explores the increase in the number of endemic Cerrado species in recent years (2000-2020) and biogeographic patterns typically associated with species of restricted distribution in the face of accelerated land use changes on natural habitats. The chapter emphasizes that the accelerated pace of describing new endemic terrestrial vertebrate species in the Cerrado is not accompanied by conservation efforts, particularly for recently described species with restricted distribution. The second chapter proposes a regionalization approach to identify 29 regions with groups of co-distributed species forming the basis for discussions on the origin and evolution of the unique biotas of the Cerrado. The results are compared with patterns previously detected with distribution data of amphibians and Squamata

reptiles, revealing potential generalization of the detected pattern for different groups of terrestrial vertebrates. Lastly, the third chapter proposes priority areas for the conservation of the analyzed species and discusses the effect of changes in land use between 1985 and 2020 on the detection of priority areas for the conservation of the endemic vertebrate fauna of this savanna, which is the richest and most threatened on the planet.

Keywords: Cerrado, Endemism, Regionalization, Conservation, Hotspot.

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Introdução Geral

Estudos em biogeografia são destinados a elucidar a distribuição geográfica dos organismos e compreender como essas distribuições estão relacionadas com as áreas que esses organismos ocupam (Carvalho & Almeida, 2016). Uma distribuição geográfica é a compilação de todos os registros conhecidos de uma espécie. Em geral, mapear essa distribuição nos ajuda a perceber padrões espaciais simples relacionados, por exemplo, à ocorrência de variações populacionais e a potenciais limites de distribuição (Gaston, 2003). As distribuições geográficas das espécies podem ser limitadas por fatores históricos – processos ligados a escalas profundas de tempo como história da terra e dinâmica climática histórica das áreas que habitam – e/ou ecológicos – ligados a fatores intrínsecos da espécie e das espécies com as quais ela interage (C. B. Cox, Moore, & Ladle, 2016), e de variáveis ambientais contemporâneas. Espécies que possuem distribuições limitadas associadas exclusivamente em uma dada região do globo são reconhecidas como endêmicas dessa região (C. B. Cox et al., 2016). Ao analisar detalhadamente a distribuição geográfica de várias espécies, endêmicas ou não de uma dada região, é possível detectar padrões gerais de distribuição da diversidade (J. H. Brown, 1995), o que contribui para a discussão sobre os papéis de fatores históricos e ecológicos na geração de biotas, e também aprimora o processo de tomada de decisão para fins de conservação (Hausdorf, 2002; Whittaker et al., 2005). No entanto, a maioria das análises que visam detectar áreas prioritárias globais para a conservação da biodiversidade depende do endemismo de plantas ou vertebrados como medida central de importância biológica (Brooks et al., 2006). Como exemplo clássico, os *Hotspots* de Biodiversidade são ecorregiões globais caracterizadas por concentrações excepcionais de espécies endêmicas e altos níveis de perda de habitat (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000). Apesar das limitações em relação à análise em escalas mais finas, a detecção de *hotspots* com base em endemismo tem direcionado eficientemente a atenção da comunidade científica e de tomadores de decisão para as regiões mais insubstituíveis e ameaçadas do mundo (Brooks et al., 2006; Reid, 1998).

Além da detecção de padrões de distribuição de endemismos ser essencial para a fundamentação muitas estratégias de priorização para conservação (Brooks et al., 2006), trata-se de um elemento chave na busca de fatores que geram os padrões de regionalização. Há séculos a ciência se dedica a compreender os fatores que geram os padrões de distribuição e abundância dos organismos pelo globo (J. H. Brown, 1995). A argumentação sobre como diferentes áreas do globo são ocupadas por diferentes componentes faunísticos data pelo menos da metade do século XVIII com a proposição da “Lei de Buffon” pelo naturalista francês Georges-Louis Leclerc (“conde de Buffon”), e seguiu sendo estruturada no século seguinte nos trabalhos de Philip Lutley Sclater e Alfred Russel Wallace que estabeleceram os alicerces da ciência conhecida atualmente como regionalização bioge-

gráfica (ver [C. B. Cox et al., 2016](#)). Essas conclusões prévias sobre as grandes biorregiões globais ainda são amplamente aceitas, e propostas mais recentes diferem em poucos detalhes do que foi sugerido séculos antes, mesmo com o surgimento de novos métodos de análise e com acúmulo de informações sobre o parentesco dos grupos analisados (e.g. [Holt et al., 2013](#)). Isso consolida o entendimento sobre uma dada área e estimula avanços para questões posteriores, como por exemplo para discussões em torno do reconhecimento e delineamento dos limites de cada região (e.g. [Ficetola, Mazel, & Thuiller, 2017](#); [Morrone, 2018](#)) e favorece o direcionamento dos esforços de pesquisa para áreas aplicadas, com consequente produção de material para a formulação de políticas públicas mais eficientes ([Brooks, da Fonseca, & Rodrigues, 2004](#); [Whittaker et al., 2005](#)). Porém, estudos comparativos sobre a estruturação de regiões biogeográficas em escala local, mais refinadas, são proporcionalmente mais escassos e carecem de testes quanto à generalização das regiões propostas.

As interpretações sobre padrões biogeográficos históricos dependem primariamente da delimitação eficiente de unidades biogeográficas ([Hausdorf, 2002](#)). No entanto, a escassez e imprecisão de dados de base sobre a distribuição de organismos (Impedimento Wallaceano) tende a dificultar a definição e o delineamento de unidades biogeográficas, especialmente em regiões de elevada diversidade biológica ([Ficetola et al., 2014](#)) e em escalas mais refinadas de análise ([Whittaker et al., 2005](#)). De acordo com Nelson e Platnick ([1981](#)), as dificuldades associadas à delimitação de unidades biogeográficas deveriam reduzir caso um grupo numeroso e diverso de táxons fosse analisado quanto à co-ocorrência de espécies. Isso por que acredita-se que os processos geológicos que modificam grandes áreas podem afetar de modo similar a distribuição de diferentes conjuntos de organismos ([Wiley, 1988](#)), de modo que estes tendem a compartilhar áreas de distribuição bastante similares entre si ([Hausdorf, 2002](#)). Essa ideia destaca a importância de analisar as distribuições de uma amostra representativa dos organismos conhecidos de uma região para identificarmos padrões robustos de distribuição e compreendermos melhor tanto a sua origem, quanto a das áreas que ocupam ([Morrone, 2002](#); [Wiley, 1988](#)).

O Cerrado é considerado o maior representante de ambientes savânicos nos neotrópicos ([Silva & Bates, 2002](#)), além de ser a savana mais rica (em número de espécies) e ameaçada do planeta ([Klink & Machado, 2005](#)). No entanto, dos aproximadamente 200 milhões de hectares que o Cerrado abrange, apenas 19,8% se mantém intacto, e menos de 11% estão legalmente protegidos, dos quais, menos que 3% são unidades de conservação de proteção integral ([Strassburg et al., 2017](#); [Vieira-Alencar et al., 2023](#)). Mais de 4.800 espécies de plantas e vertebrados são encontrados apenas no Cerrado, portanto, endêmicas dessa ecorregião ([Strassburg et al., 2017](#)), que apesar de ser considerado um hotspot de biodiversidade ([Myers et al., 2000](#)), ainda sofre pressão da expansão de atividades agropecuárias e de ocupação humana ([Klink & Machado, 2005](#); [Strassburg et al., 2017](#)). Apesar das primeiras interpretações faunísticas do Cerrado terem descrito faunas

empobrecidas e com baixo grau de endemismo (ver revisão em Nogueira, Colli, Costa, & Machado, 2010), esforços direcionados para melhor compreensão da sua biodiversidade revelaram que essas interpretações não só subestimavam a riqueza dessa savana, como negligenciavam a existência de padrões biogeográficos formados por espécies com distribuições geográficas restritas (ver Nogueira et al., 2010), cuja capacidade de detecção é consideravelmente menor (Gaston, 1996). Isso é ainda mais evidente quando consideramos a proporção crescente de espécies novas descritas para a região nas últimas décadas (ver Nogueira et al., 2010), o que apesar de ampliar o conhecimento faunístico, revela padrões biogeográficos sob ameaça diante do cenário atual de uso da terra (Strassburg et al., 2017; ver [Hotspot getting hotter](#)). Isso enfatiza a importância de se expandir o conhecimento sobre a distribuição da biota e padrões biogeográficos em escalas mais refinadas, com potencial para generalizações e comparações futuras, ampliando a eficiência na tomada de decisão para a conservação do Cerrado (Diniz-Filho, Bini, Pinto, et al., 2008). Com as ameaças à biodiversidade do Cerrado sendo discutidas de maneira contundente na comunidade científica (e.g Klink & Machado, 2005; P. Pacheco et al., 2021; Strassburg et al., 2017; Velazco, Villalobos, Galvão, & DeMarco Jr., 2019), torna-se primordial a necessidade de manter atualizado o conhecimento biogeográfico, botânico e faunístico dessa região, uma vez que, considerando-se a heterogeneidade inerente às ecorregiões brasileiras (Bridgewater, Ratter, & Ribeiro, 2004; Ratter, Bridgewater, & Ribeiro, 2003), nem a biodiversidade nem as ameaças são distribuídas igualmente por todo seu território (Azevedo, Valdujo, & Nogueira, 2016; Carmignotto, Pardini, & de Vivo, 2022; Klink & Machado, 2005; Nogueira, Ribeiro, Costa, & Colli, 2011; Ratter et al., 2003).

Entre as primeiras interpretações biogeográficas do Cerrado, estão as que usaram o conhecimento corrente na época sobre a distribuição de aves (Silva, 1995, 1997; ver, porém Müller, 1979; Vanzolini, 1963), grupo tradicionalmente melhor amostrado e com melhores dados de distribuição e taxonomia (J. H. Brown, 1995). De modo geral, aves apresentam ampla capacidade de dispersão (Sick, 1997), e tendem a apresentar as mais amplas distribuições entre os vertebrados (Gaston, 1996), o que pode mascarar padrões de distribuição originados por vicariância (Hausdorf, 2002). No entanto, diversos táxons são conhecidos como especialistas de habitat dentro do domínio Cerrado, e espécies como *Paroaria baeri* (Cardeal-do-Araguaia), *Pyrrhura pfrimeri* (Tiriba-de-pfrimeri) e *Scytalopuss novacapitalis* (Tapaculo-de-Brasília), entre outras, apresentam áreas de distribuição restritas (Gwynne, Ridgely, Tudor, & Argel, 2010), o que torna certos taxa interessantes do ponto de vista biogeográfico (Silva, 1997). Pequenos mamíferos são abundantes e caracterizados por apresentar alta seletividade de habitats (Carmignotto & Aires, 2011), o que é considerado um dos fatores que historicamente restringiu as distribuições de populações em diferentes áreas do Cerrado (Carmignotto et al., 2022), e pode adicionar maior detalhamento aos padrões biogeográficos já conhecidos. Assim, esperamos que com a análise de dados de distribuição de aves e pequenos mamíferos, combinados com os dados de

distribuição de espécies descritas desde a última atualização da base de anfíbios e Squamata usada por Azevedo et al. (2016), seja possível testar a validade das regiões descritas por esses autores (e.g. Azevedo et al., 2016; Nogueira et al., 2011; Silva, 1997), bem como possivelmente detectar novas regiões (Carvalho & Almeida, 2016; ver [Cerrado endemic tetrapod bioregions](#)) além de tornar possível detectar não apenas padrões específicos a cada grupo de vertebrado, como nesses estudos anteriores, mas padrões biogeográficos gerais mais robustos, que possivelmente se repetem em outros grupos ainda não estudados, e que decorrem de processos amplos, geradores de especiação e biodiversidade (Morrone, 2002; Wiley, 1988). Com avanços recentes tanto em relação à taxonomia e filogenia e o desenvolvimento de métodos sofisticados de análise e ferramentas avançadas de processamento de dados espaciais, podemos analisar um número elevado e diverso de espécies endêmicas se aproximando não só de conclusões mais robustas sobre a história do Cerrado como também dos processos geradores de biodiversidade dessa ecorregião.

Espécies endêmicas, especialmente as que possuem distribuições confinadas em áreas mais restritas de uma dada região, são intrinsecamente mais sujeitas à declínios populacionais causados por ameaças externas, como a perda de habitat e as mudanças climáticas globais (Gaston, 1998). Além disso, esse elevado grau de associação a uma dada área representa um fator de risco pela potencial exposição de toda a espécie a fatores puramente estocásticos (e.g. aleatórios), mesmo que ocorram em escala local (Gaston, 1998, 2003). Sintetizar informações robustas sobre a distribuição de tetrapoda endêmicos do Cerrado nos permitiria, por exemplo, avaliar padrões gerais de perda de habitat dessas espécies e o grau de proteção fornecido pela rede atual de unidades de conservação, o que é relevante especialmente as descritas mais recentemente, que em geral possuem áreas de distribuição mais restritas (Gaston, 1996). Assim, poderíamos mapear as regiões do Cerrado marcadas pelo avanço recente em conhecimento taxonômico, regiões em que as espécies vêm sendo mais impactadas pela conversão de habitats naturais e regiões que concentram espécies não contempladas pela rede atual de unidades de conservação (ver [Hotspot getting hotter](#)). Desse modo, podemos posteriormente otimizar os esforços para conservação da biodiversidade (Whittaker et al., 2005), favorecendo a alocação de recursos de maneira direcionada e eficaz, e assim, aumentando a representatividade da biodiversidade a ser protegida (Brooks et al., 2006). Representar diferentes componentes da biodiversidade em estratégias sistemáticas de conservação é mandatório especialmente em áreas de elevada insubstituibilidade e vulnerabilidade. Áreas que se enquadram nessa categoria são ocupadas sobretudo por espécies raras e/ou com distribuições restritas, geralmente em regiões sob ameaça de serem alteradas (e.g. áreas não protegidas legalmente Brooks et al., 2006). Com essas informações seria possível propor áreas prioritárias à conservação de forma sistemática de modo a favorecer maior representação da biodiversidade (ver [Priority Areas of Cerrado hotspot](#)). Aqui, buscamos (a) sintetizar o conhecimento existente sobre espécies de vertebrados terrestres (tetrapodas) endêmicos do Cerrado, (b)

avaliar a distribuição geográfica dessas espécies em relação à sua área, perda de habitat e proteção em unidades de conservação, (c) compreender a situação da avaliação sobre o risco de extinção dessas espécies também em relação às variáveis mencionadas acima, (d) detectar e mapear regiões biogeográficas caracterizadas pela co-ocorrência de espécies de vertebrados terrestres endêmicos e comparar essa regiões com as detectadas em estudos anteriores, e por fim (e) detectar e mapear áreas prioritárias à conservação das espécies aqui estudadas, além de (f) avaliar como essas áreas prioritárias se modificaram ao longo do tempo em detrimento das mudanças no uso do solo da savana mais rica e ameaçada no planeta.

Daqui em diante o texto da tese seguirá majoritariamente em inglês, com exceção apenas para dois *disclaimers* relacionados ao capítulo 3, e às conclusões gerais advindas nos estudos específicos de cada capítulo. Espero que a leitura dos artigos também seja proveitosa, mas se optar por pular essa parte mais quadrada, nos vemos nas conclusões gerais onde devo explicar de forma resumida o que encontramos a seguir.

¹ 1 Hotspot getting hotter: the rise in endemism levels and habitat loss and the plight of the Cerrado savannas

²

Abstract

³ The Cerrado hotspot is the second largest neotropical ecoregion and the richest and most
⁴ threatened savanna in the globe, having been recognized as a global biodiversity hotspot
⁵ due to the high number of endemic plant species and high rates of deforestation. Herein
⁶ we synthesise recent advances in taxonomical and biogeographical knowledge of endemic
⁷ terrestrial vertebrates (tetrapods) in the Cerrado, coupled with an update on current levels
⁸ of threat, habitat loss and protection for these endemic biotas. New tetrapods have been
⁹ described throughout the Cerrado at an average rate of six species per year in the last two
¹⁰ decades, and the most recently discovered show restricted ranges. Most new species were
¹¹ described from already highly impacted regions and almost half of all endemic tetrapod
¹² species showed less than 50% of their range covered by natural habitats. Moreover, more
¹³ than 87% of the species showed less than 17% of their ranges within protected areas,
¹⁴ highlighting protection gaps in the Cerrado. Finally, our results indicate that threatened
¹⁵ species lists in the Cerrado are probably underestimated, with high numbers of data-
¹⁶ deficient species impacted by habitat loss and lacking protection. Our results indicate
¹⁷ that urgent conservation action is badly needed to halt biodiversity loss in the most
¹⁸ threatened savanna of the World.

¹⁹ **Keywords:** Biodiversity Conservation, Threat assessment, Extinction, Gap analysis,
²⁰ Grasslands, Vertebrates

21 1.1 Introduction

22 Most analyses of global priority areas for biodiversity conservation rely on plant or
23 vertebrate endemism as a central measure of biological importance (Brooks et al., 2006).
24 As a classical example, Biodiversity Hotspots are global-scale ecoregions characterised by
25 exceptional concentrations of endemic species and high levels of habitat loss (Mittermeier,
26 Myers, Thomsen, Fonseca, & Olivieri, 1998; Myers, 1988, 1990; Myers et al., 2000). Des-
27 pite the limitations regarding finer-scale analysis, the hotspot framework has efficiently
28 directed scientific attention toward the most irreplaceable and endangered regions of the
29 world (Brooks et al., 2006; Reid, 1998).

30 Biodiversity conservation priorities, both at global or regional scales, are often de-
31 fined based on the combination of vulnerability (extrinsic threats) and irreplaceability
32 (intrinsic biological importance, see Brooks et al., 2006). The biodiversity hotspot con-
33 cept has been recognised as a highly relevant global biodiversity conservation strategy,
34 and when compared to other conservation global priority templates based on the irrepla-
35 ceability x vulnerability framework (Brooks et al., 2006; Ginsberg, 1999) is considered a
36 reactive approach, highlighting areas in need of urgent action due to combined high levels
37 of threat (vulnerability) and richness of endemics (irreplaceability, Brooks et al., 2006).

38 In a classical study of conservation biogeography, Myers et al. (2000) recognized 25
39 biodiversity hotspots where they believed that conservation efforts should be concentrated,
40 and the largest neotropical savanna, the Cerrado, was pointed as one of those regions. In
41 fact, in an earlier sketch of the classical hotspot paper (Myers et al., 2000), Mittermeier et
42 al. (1998) already mentioned the Cerrado savannas as a putative biodiversity hotspot in
43 what they called ‘initial conclusions’ (Mittermeier et al., 1998). More recently the revised
44 list of global hotspots (Mittermeier et al., 2004) was expanded to 34 areas, including the
45 Cerrado (see also Willians et al., 2011, for the addition of the 35th hotspot).

46 The definition of global Biodiversity Hotspots depends on a fundamental bioge-
47 graphical concept: endemism. Endemic species are those occurring exclusively within a
48 specific area or region (Nelson & Platnick, 1981), and the co-occurrence of at least two
49 of such species delimits the basic units for analyses of the evolution of biotas (Nelson
50 & Platnick, 1981). More importantly, the presence of endemic species is an indicator of
51 potential in situ speciation, linking the presence of taxa to evolutionary events that took
52 place within (or as a result of) that particular area (Harold & Mooi, 1994). As endemic
53 species are exclusive to particular, often confined areas, they also indicate patterns of
54 biotic turnover and regionalization (Harold & Mooi, 1994; Hausdorf, 2002), defining areas
55 of high spatial irreplaceability and high conservation priority (Brooks et al., 2006; Lamo-
56 reux et al., 2006). Finally, endemic species are intrinsically vulnerable to extinction, given
57 their spatial rarity and often small, specialised ranges (Gaston, 1998). As such, endemic
58 species are of high conservation concern due to three intertwined biogeographical aspects:

59 evolutionary significance, intrinsic vulnerability, and high irreplaceability.

60 However, the detection of global hotspots does not depend on fine-scale distribution
61 data or detailed mapping of areas of endemism or regionalization patterns. Instead, lists
62 of recorded and endemic taxa are compiled and compared, based simply on the presence
63 of taxa within large global ecoregions (Mittermeier et al., 1998; Myers, 1988, 1990; Myers
64 et al., 2000). This can be seen as a strength of the method, capable of delivering re-
65 sults without the aid of detailed, time-consuming and often unavailable compilations of
66 fine-scale data on species occurrences. However, this same simplicity can be seen as a li-
67 mitation, as effective action at the site scale heavily depends on high-quality, fine-grained
68 species distribution data, especially for threatened or restricted-range species (Brooks et
69 al., 2006; Eken et al., 2004).

70 By the time of the classic hotspots paper (Myers et al., 2000) when the first 25
71 biodiversity hotspots were proposed, an estimation of 4,400 (from $10,000 = 44\%$) vascular
72 plant species and a total of 117 terrestrial vertebrate species (from $1268 = 9\%$) were
73 listed as endemic to the Cerrado (Myers et al., 2000). At that moment, the Cerrado
74 was still poorly studied in terms of vertebrate diversity and endemism (Colli, Vieira,
75 & Dianese, 2020; Nogueira et al., 2010), wide sampling gaps were prevalent in most
76 of the region (Cavalcanti & Joly, 2002; Colli, Bastos, & Araujo, 2002; Macedo, 2002;
77 Marinho-Filho, Rodrigues, & Juarez, 2002), and, as a result, preliminary interpretations
78 pointed to a homogeneous, species-poor vertebrate fauna in central Brazilian savannas
79 (Sick, 1965; Vanzolini, 1963). However, these early conclusions of low vertebrate endemism
80 have been abandoned in recent decades, with the accumulation of faunistic inventories,
81 taxonomic discoveries describing hundreds of endemic tetrapod species, and new faunistic
82 syntheses (Azevedo et al., 2016; Carmignotto et al., 2022; Gutiérrez & Marinho-Filho,
83 2017; Nogueira et al., 2019, 2010; Nogueira, Colli, & Martins, 2009; Valdujo, Silvano,
84 Colli, & Martins, 2012, present study).

85 Meanwhile, despite the call to direct urgent conservation action to biodiversity hots-
86 pots, the Brazilian Cerrado has lost more than 50% of its native vegetation cover, a rate
87 nearly 2.5 higher than in Amazonia, and less than 11% of the ecoregion is under the
88 protection of the current protected areas network, considering all protected area catego-
89 ries (Strassburg et al., 2017; UNEP-WCMC & IUCN, 2023; Vieira-Alencar et al., 2023).
90 Moreover, the Cerrado is currently highlighted as one of the eight most threatened De-
91 forestation Frontiers of the world (P. Pacheco et al., 2021). The rise in basic faunistic
92 knowledge, coupled with the constant high rates of habitat loss, poses a serious and urgent
93 challenge for conservation planning and biodiversity science: what are the effects of the
94 extreme habitat loss and fragmentation on the newly discovered endemic vertebrates in
95 the Cerrado? Given their intrinsic vulnerability (especially in a scenario of rapid habitat
96 loss, see Strassburg et al., 2017), their importance as indicators of historical processes and
97 their presence in highly irreplaceable sites and areas, we herein provide the first detailed

98 and comprehensive analysis of the conservation of currently described Cerrado endemic
99 tetrapods. Our major goal is to measure and contrast the important recent scientific
100 advances in taxonomy and zoogeographical documentation with the current scenario of
101 extensive and fast land use changes, especially in the last two decades since the publication
102 of the classical hotspot paper ([Myers et al., 2000](#)).

103 More specifically, we aim to a) to quantify and map endemism levels based on
104 the most up-to-date endemic terrestrial vertebrates point-locality record database, in
105 comparison to data in the classical hotspots paper ([Myers et al., 2000](#)); b) to assess current
106 levels of habitat loss and its impact on recently discovered Cerrado endemic biotas; c) to
107 assess the level of protection and possible conservation gaps in Cerrado endemic tetrapods;
108 d) to assess and compare the threat status of Cerrado endemic tetrapods according to the
109 global and national Red Lists; and e) to test if Cerrado endemic terrestrial vertebrates
110 follow the general macroecological trend of restricted ranges in recently described species.
111 Are these endemic species well represented in the current protected area system? Are
112 intrinsic and extrinsic indicators (range size, date of description and area of remaining
113 habitat) well incorporated in recent threat assessments for these endemic species? Based
114 on these analyses, we aim to investigate if recent advances in biodiversity documentation
115 in the Cerrado are properly reflected in biodiversity assessments and conservation actions,
116 providing scientific and spatial guidance for urgent conservation measures in the richest
117 and most impacted savanna on the planet.

118 1.2 Materials and Methods

119 1.2.1 Study area

120 The Cerrado is the largest savanna in the Neotropics and the most diverse tropical
121 savanna on the planet ([Klink & Machado, 2005](#); [Ratter, Ribeiro, & Bridgewater, 1997](#)).
122 We considered the Cerrado limits as in [Dinerstein et al. \(2017\)](#) with minor modifications
123 to facilitate mapping of marginal peripheral relicts. This grassland and savanna ecoregion
124 occupies a central position in South America, dominating ancient uplands of the Brazilian
125 shield, separating lowland open areas of the Caatinga in the northeast from the Chaco
126 in the southwest, while also separating the Amazonian Forests in the northwest from
127 the Atlantic Forest in the southeast ([Silva & Bates, 2002](#)). The Cerrado vegetation is
128 dominated by fire-resistant savannas and grasslands, associated with upper, highland
129 portions of major drainages of South America (Tocantins-Araguaia, Paraná, Paraguay,
130 Guaporé, and São Francisco, [Ab'Sáber, 1998](#)).

131 These topographical and edaphic conditions generate a complex mosaic of habitats,
132 with grassland and savannas crossed by palm marshes and gallery forests along drainages
133 ([Eiten, 1972](#); [Ratter et al., 1997](#)), a pattern observed both at local and continental scales,

134 forming complex, horizontally stratified landscapes, whose character and evolution are
135 strongly tied to the geomorphology of major plateaus and depressions of central portions
136 of South America (Colli et al., 2020; Silva & Bates, 2002). As a result, Cerrado faunas are
137 rich and complex assemblages both at the local and regional scales, dominated by habi-
138 tatt specialist species segregated according to horizontally stratified and widely divergent
139 major habitat types (Carmignotto et al., 2022; Nogueira et al., 2009; Silva, 1997; Silva
140 & Bates, 2002). At the regional scale, Cerrado faunas are distributed in a non-random,
141 regionalized pattern, with groups of co-distributed species forming allopatric biotas and
142 areas of endemism, strongly determined by topography and geomorphology (Azevedo et
143 al., 2016; Nogueira et al., 2011; Silva & Bates, 2002; Valdujo et al., 2012).

144 1.2.2 *Species distribution and threat assessment data*

145 We updated the list of Cerrado endemic terrestrial vertebrate species presented in
146 previous studies (Azevedo et al., 2016; Carmignotto, Vivo, & Langguth, 2012; Gutiérrez
147 & Marinho-Filho, 2017; Nogueira et al., 2011; Silva, 1997) considering as endemic those
148 species whose ranges are fully or largely coincident with the approximate limits of the
149 Cerrado. Species found in the Cerrado core area but with marginal records in transitional
150 areas between the Cerrado and adjacent domains, and with local ranges associated with
151 typical Cerrado environments, were also considered endemic. We included in our analyses
152 the geographical ranges of species described up to early January 2021. The absolute
153 number of terrestrial vertebrate species occurring in the Cerrado was obtained from the
154 most recent national assessment of threatened species (ICMBio, 2023), and compared to
155 those reported in Myers et al. (2000). The taxonomy follows specific literature for each
156 vertebrate group (Frost, 2020 for anurans, Uetz, Freed, Aguilar, Reyes, & Hosekm, 2020
157 for lizards/amphisbaenians, Nogueira et al., 2019 for snakes, J. F. Pacheco et al., 2021 for
158 birds, and Abreu et al., 2021 for mammals).

159 Our major data source is a revised point locality database for Cerrado endemic
160 tetrapods, compiled over the last two decades (see details in Carmignotto et al., 2022;
161 Nogueira et al., 2019, 2009, 2011; Valdujo et al., 2012). Our database was built based
162 on: 1) planned field surveys in previous sampling gaps started in the early 2000s; 2)
163 revision of vouchered specimens deposited in scientific collections, including contributions
164 to the description of new taxa and improvements in distribution mapping, and 3) revised
165 literature data, mostly from taxonomic studies and peer-reviewed species distribution
166 expansions with vouchered specimens.

167 To assess a general measure of species range we created Minimum Convex Polygons
168 (MCPs) or buffers of 10 km² around species records. Species known from less than three
169 records were mapped using buffers, and the choice between MPCs or buffers for species
170 with more than three records was based on a case-by-case analysis: species with sparse,
171 scattered, rarefied records (indicating potentially disjunct ranges and large expanses of

172 non-occupied areas) were mapped using buffers instead of MCPs. The 10 km² buffer was
173 chosen based on the IUCN guidelines to represent sensitive species ranges ([IUCN Red](#)
174 [List Technical Working Group, 2021](#)).

175 In order to gather data on the threat status of Cerrado endemic vertebrate species
176 we collected information from the global threat assessment (species assessed between April
177 2004 and November 2021; [IUCN, 2023](#), hereafter IUCN Red List) and from the Brazilian
178 official Red List (species assessed between April 2012 and October 2022; [ICMBio, 2023](#),
179 hereafter ICMBio Red List). We compared both lists on their completeness and propor-
180 tions of threat categories. However, for further analyses, we used only data from the more
181 recent and comprehensive ICMBio Red List.

182 1.2.3 *Spatial Patterns: Land-use/Land-cover (LULC) and richness*

183 We mapped LULC conversion from natural to anthropic uses between 2000 and 2020
184 using the [MapBiomas \(2022\)](#) land-cover database, covering the Cerrado in the Brazilian
185 territory. Then, we calculated the area of remaining natural vegetation within the ranges
186 of each endemic terrestrial vertebrate species in 2000 and in 2020, using the Google Earth
187 Engine tool ([Gorelick et al., 2017](#)).

188 We calculated endemic species richness spatial patterns in each cell of a 1° × 1° grid
189 covering the Cerrado, using the Biodiverse software ([Laffan, Lubarsky, & Rosauer, 2010](#)).
190 We mapped the overall richness of endemics described up to early January 2021 and
191 subtracted endemic richness values of species described until 2000 from those in 2020 to
192 highlight areas of the recent increase in endemism levels. To identify hotspots of endemic
193 species with higher and lower levels of habitat loss we mapped the richness of species
194 with less than 30% or more than 80% of natural areas within their range. The lower
195 threshold (30%) was based on the recently proposed conservation target for the post-
196 2020 global biodiversity framework, ([Woodley et al., 2019](#)), with the higher threshold
197 (80%) representing a conservative approach to define high ecosystem integrity, given the
198 lower accuracy of satellite image classification in capturing natural open formations in the
199 Cerrado ([Alencar et al., 2020](#)). Finally, we mapped the richness of species whose ranges
200 are not represented in any strict protection protected area (hereafter ‘gap species’) to
201 detect protection gaps in the Cerrado (see gap analysis details below).

202 1.2.4 *Gap analysis*

203 To assess the degree of protection provided by the current Cerrado protected areas
204 (PAs) network we selected all existing strict protection PAs (IUCN categories I-IV; here-
205 after, ‘PAs’ refer only to strict protection units) from the World Database of Protected
206 Areas ([UNEP-WCMC & IUCN, 2023](#)) with partial or total extension within the Cerrado
207 limits. We then calculated the proportion of each range represented within PAs. Only

208 PAs with detailed geographic information were considered, excluding those represented
209 only as points. We considered only strict protection PAs due to the limitations of Sustai-
210 nable Use PAs in protecting natural habitats in the Brazilian Cerrado (Françoso et al.,
211 2015). In addition, we mapped the richness of species whose ranges were not represen-
212 ted in any PA (hereafter ‘gap species’) to highlight regions with protection gaps in the
213 Cerrado. Conversely, large PAs ($> 100,000$ ha) were intersected with the ranges of all
214 analysed species in order to quantify endemic species richness represented in these units
215 and to highlight potential Key Biodiversity Areas for the Cerrado (KBA Standards and
216 Appeals Committee of IUCN SSC/WCPA, 2022).

217 1.2.5 Statistical analyses

218 To assess the relationship between range sizes and description dates, and to test the
219 hypothesis that recently described species tend to show relatively small, localised ranges
220 (see Gaston, 1996), we fitted a linear model of log-transformed species range sizes as a
221 function of year of species description.

222 For the tests using the Brazilian official Red List threat categories (ICMBio, 2023),
223 we compared two groups of species defined as in Borgelt, Dorber, Høiberg, and Verones
224 (2022): threatened species (all species classified as VU, EN and CR) and non-threatened
225 species (all species in LC and NT). To assess the effect of species in the DD category
226 we performed additional comparisons including all IUCN categories when specifically
227 mentioned.

228 To test if threatened x non-threatened species (Borgelt et al., 2022) are homogene-
229 ously distributed amongst tetrapod classes we compared their absolute numbers in each
230 of the four tetrapod classes via a chi-square test. In addition, we tested if threatened
231 and non-threatened species differ in range sizes, via a Kruskal-Wallis test, testing the
232 hypothesis that restricted-range species are significantly more prone to be classified as
233 threatened than widespread taxa. To assess possible differences in range size related to
234 the numbers of DD species we repeated this same test including all categories.

235 We compared threatened and non-threatened species according to the proportion of
236 the current area of remaining natural habitats within their ranges, via a Kruskal-Wallis
237 test, testing the hypothesis that Red List categories are correctly capturing the impact of
238 habitat loss on endemic species. Although we recognize that not all remaining vegetation
239 is equivalent to occupied habitat, we used this general measure as a proxy for habitat
240 quality and extent, given the limited amount of information on actual remaining habitats
241 and local distribution of many studied species. Furthermore, we tested if threatened
242 and non-threatened species differ in terms of the proportion of their range represented
243 within the current PA network, also via a Kruskal-Wallis test, testing the hypothesis that
244 threatened species are significantly less represented in protected areas. To assess possible

245 differences in protection related to the numbers of DD species, we repeated this same test
 246 now including all categories.

247 1.3 Results

248 1.3.1 *The rise in endemism levels of Cerrado tetrapods*

249 According to our synthesis, a total of 2047 terrestrial vertebrate species are known
 250 to occur in the Cerrado. We considered 340 as endemics, including 124 amphibians,
 251 129 reptiles, 45 birds and 42 mammals. Compared to the data presented by Myers et al.
 252 (2000), these values represent an increase of 61.4% in the total number of tetrapod species
 253 (1268 to 2047) and of 190.6% in the number of endemics (117 to 340) in the Cerrado. In
 254 the last two decades, numbers and percentages of endemics rose in all tetrapod classes
 255 but were higher in amphibians and reptiles (Figure 1), the two classes that also show
 256 the highest absolute number and proportion of endemics. Although in mammals the
 257 percentage of endemic species showed only a slight increase, the absolute number of
 258 endemics more than doubled since 2000 (19 to 42 species).

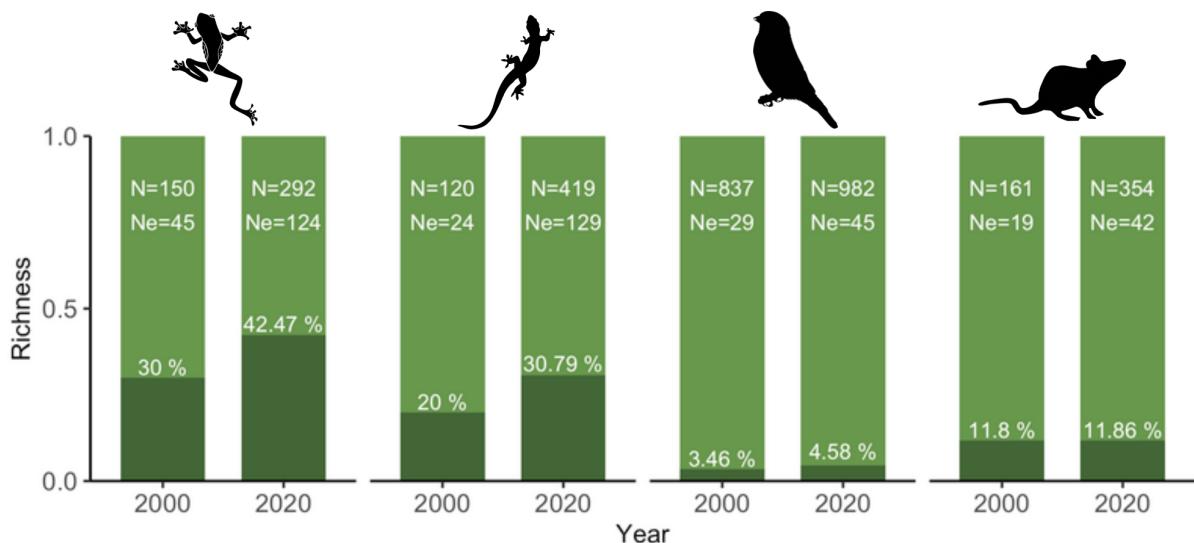


Figure 1 – Numbers and proportions of Cerrado endemic species (dark green) in each tetrapod class in two time slices: 2000 (According to Myers et al. 2000) and 2020 (present study for endemics; ICMBio, 2023 for non-endemics).

259 1.3.2 *Evolution of taxonomic knowledge*

260 Of all 340 Cerrado endemic terrestrial vertebrates, 132 (38.8%) were described re-
 261 cently, between 2000 and early January 2021, while 137 (40.3%) were described between
 262 1900-1999, and the remaining 71 taxa (20.9%) were early descriptions between 1700-1899.
 263 The rate of species descriptions since 1820 was of 2.74 species each year but showed a

264 strong acceleration in the last two decades, with an average of six species described each
 265 year after the 2000s ([Figure 2](#)).

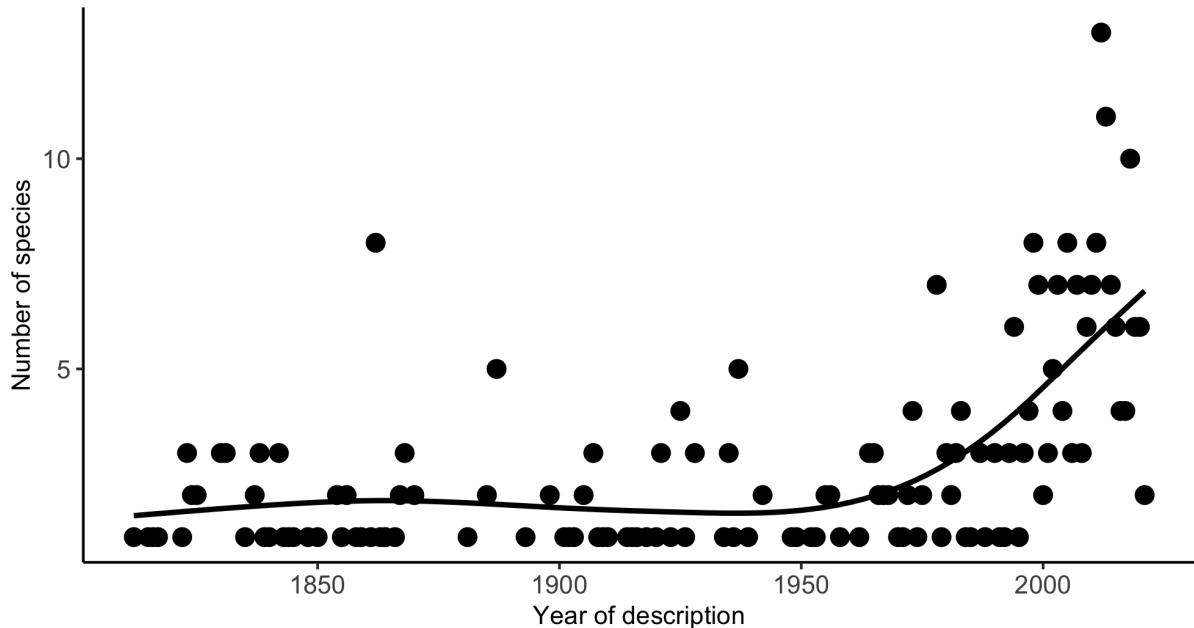


Figure 2 – Number of species of Cerrado tetrapods described from the early taxonomic studies of the XVIII century to the present.

266 1.3.3 *Hotspots within hotspots: mapping richness, discovery, habitat loss and 267 protection gap*

268 Areas of high endemic species richness are scattered across the Cerrado ([Figure 3b](#)),
 269 but concentrations of endemics (up to 91 species per cell) were found at the southeastern
 270 portion of the Cerrado (Espinhaço range), central Cerrado (Central Brazilian Plateau),
 271 southern Cerrado (São Paulo state Cerrado) and western Cerrado (near Chapada dos
 272 Guimarães plateau). Most of these areas of high endemic richness are coincident with
 273 areas heavily impacted by habitat loss, especially along the southern and southwestern
 274 portions of the Cerrado ([Figure 3a,b](#)).

275 Areas of recent (2000-2020) increase in the number of endemics are also scattered
 276 across the region ([Figure 3c](#)), but higher rates of discoveries were concentrated at the
 277 central (Central Brazilian Plateau), eastern (Espinhaço range) and northeastern (Jalapão
 278 region and Tocantins river basin) portions of the Cerrado. Except for the northeastern
 279 region, most recently described endemics were found in areas already heavily impacted
 280 by habitat loss, especially at the central and southeastern portions of the Cerrado (see
 281 [Figure 3a,c](#)).

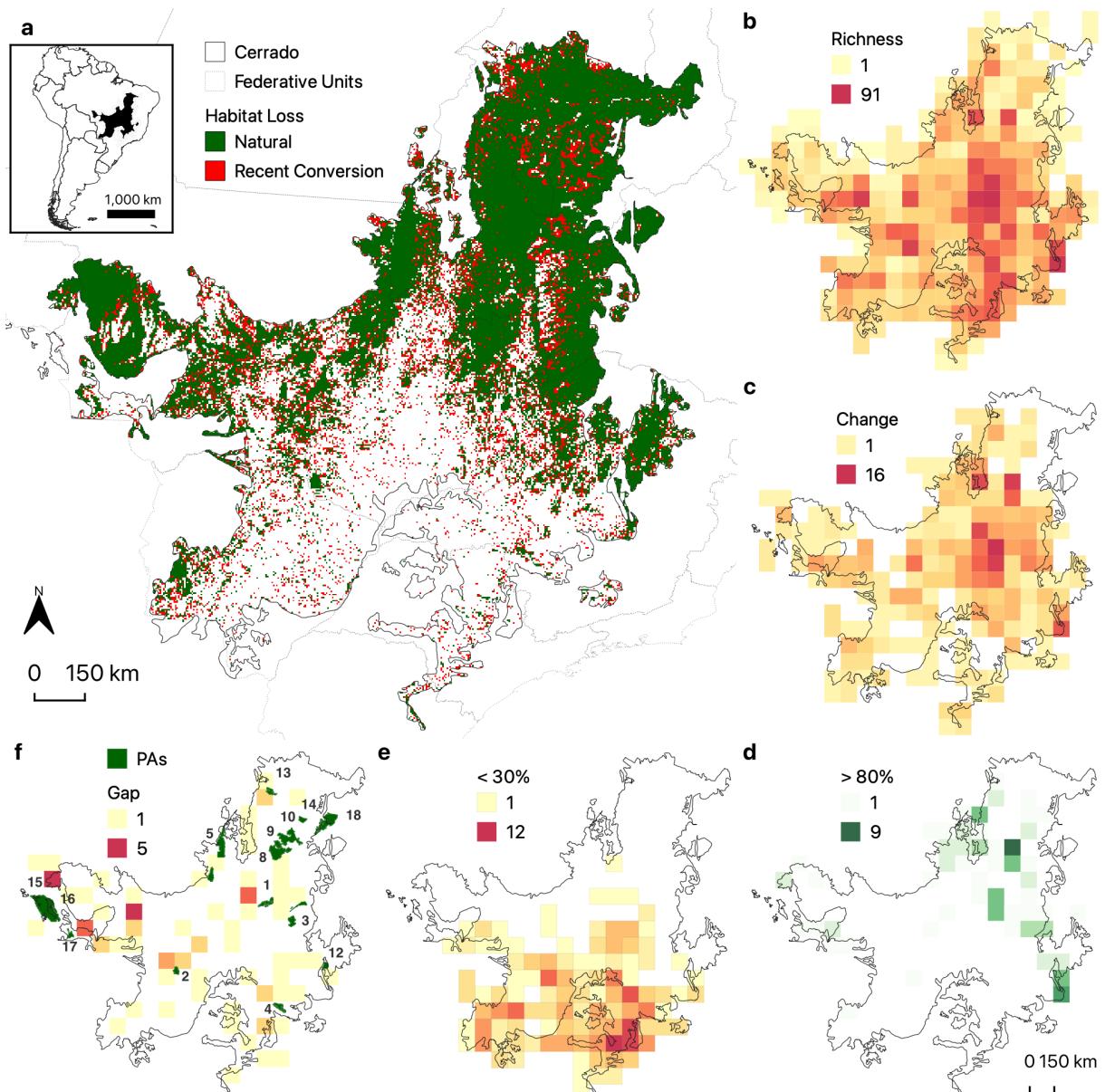


Figure 3 – Map of land-use and land-cover change from Natural to Anthropic uses in the period from 2000 to 2020, according to MapBiomas (2023) (a). Areas in white within the Cerrado limits were already under anthropic uses in 2000; Endemic tetrapod richness in 2020 (b); Increase in number of endemic tetrapod richness (2000-2020) (c); Endemic tetrapod richness of species least (d, more than 80% remaining habitats) and most (e, less than 30% remaining habitats) affected by habitat loss; and Endemic tetrapod gap species (0% range overlapping PAs) richness (f); Warmer/darker colours indicate higher values. All maps are based on a $1^{\circ} \times 1^{\circ}$ grid. Numbers in (f) stand for: 1 - Parque Nacional (PN) da Chapada dos Veadeiros; 2 - PN das Emas; 3 - PN Grande Sertão Veredas; 4 - PN da Serra da Canastra; 5 - Parque Estadual (PE) do Araguaia; 6 - Refúgio de Vida Silvestre Veredas do Oeste Baiano; 7 - Estação Ecológica (EE) Serra Geral do Tocantins; 8 - PN do Araguaia; 9 - PE do Jalapão; 10 - PN das Nascentes do Rio Parnaíba; 11 - PE do Cantão; 12 - PN das Sempre Vivas; 13 - PN da Chapada das Mesas; 14 - EE de Uruçuí-Una; 15 - PN Noel Kempff Mercado; 16 - PE Serra de Ricardo Franco; 17 - PE Serra de Santa Bárbara; and 18 - PN Serra das Confusões.

282 A clear north-south division in the Cerrado is visible in maps of species least and
 283 most affected by habitat loss ([Figure 3d,e](#)). Species with less than 30% remaining habitats
 284 within ranges are concentrated in the southern portion of the Cerrado, while species
 285 with more than 80% remaining habitats within ranges are concentrated in the north and
 286 northeastern portions of the region (see [Figure 3d,e](#)).

287 Strict protection PAs that encompasses any portion of the Cerrado started to be
 288 designated in the late 50s and the current PA network covers an area of 77,538 km² of
 289 which 49,667 km² (64%) are strictly within the Cerrado limits (representing 2.56% of the
 290 region; see PA area accumulation through time in [Supporting information - Figure S1](#)).
 291 The richest and largest PAs in the Cerrado harbour up to 108 sympatric endemic tetrapod
 292 species ([Table 1](#), see also [Figure 3f](#)) and can be pointed as candidate Key Biodiversity
 293 Areas (KBAs, see [KBA Standards and Appeals Committee of IUCN SSC/WCPA, 2022](#))
 294 for safeguarding Cerrado endemic tetrapods, with Parque Nacional Chapada dos Ve-
 295 deiros, Parque Nacional das Emas, Parque Nacional Grande Sertão Veredas and Parque
 296 Nacional da Serra da Canastra harbouring the richest Cerrado endemic tetrapod faunas
 297 (See [Table 1](#)).

Table 1 – Richest strict protection PAs in terms of Cerrado endemic terrestrial vertebrates. All strict protection PAs with more than 100,000 ha are listed. Code = PA code ID linked to [Figure 3f](#); Year = Year of PA creation; N = Number of Cerrado endemic terrestrial vertebrates whose geographical range intersects with PA limits; Area is calculated in hectares (ha).

Code	Name	Designation	Year	N	Area (ha)
1	Parque Nacional Chapada dos Veadeiros	National Park	1961	108	240,585
2	Parque Nacional das Emas	National Park	1961	99	132,785
3	Parque Nacional Grande Sertão Veredas	National Park	1989	94	230,854
4	Parque Nacional da Serra da Canastra	National Park	1972	84	197,971
5	Parque Estadual do Araguaia	State Park	2001	78	229,921
6	Refúgio de Vida Silvestre Veredas do Oeste Baiano	Wildlife Refuge	2002	78	128,050
7	Estação Ecológica Serra Geral do Tocantins	Ecological Station	2001	77	707,087
8	Parque Nacional do Araguaia	National Park	1959	75	555,503
9	Parque Estadual do Jalapão	State Park	2001	65	158,972
10	Parque Nacional das Nascentes do Rio Parnaíba	National Park	2002	60	749,770
11	Parque Estadual do Cantão	State Park	1998	60	100,414
12	Parque Nacional das Sempre Vivas	National Park	2002	57	124,156
13	Parque Nacional da Chapada das Mesas	National Park	2005	46	159,953
14	Estação Ecológica de Uruçuí-Una	Ecological Station	1981	41	135,125
15	Parque Nacional Noel Kempff Mercado	National Park	1979	37	1,617,204
16	Parque Estadual Serra de Ricardo Franco	State Park	1997	36	157,831
17	Parque Estadual Serra de Santa Bárbara	State Park	1997	33	120,432
18	Parque Nacional Serra das Confusões	National Park	1998	27	823,845

298 However, amongst the 340 endemic species analysed, 296 (87.05%) are poorly repre-
 299 sented in the PA system, with less than 17% (i.e. Aichi Target) of their ranges represen-
 300 ted in strict protection reserves. Of those, 129 (43.58%) are restricted range species, 142
 301 (47.97%) are partially ranged, and 25 (8.44%) are widespread endemic species. A total of

302 51 (15%) species are completely absent from PAs (hereafter, gap species, [Figure 3f](#)). Most
303 (47; 92.15%) of the gap species are restricted-range taxa occurring allopatrically, especi-
304 ally in the western portion of the Cerrado ([Figure 3f](#)), while the remaining 4 (7.85%) are
305 partially ranged species. The northeastern portion of the Cerrado shows only a few gap
306 species, being the least affected by habitat loss (see [Figure 3d](#)) and harbouring the largest
307 PAs (see [Figure 3f](#)). Considering gap species in the Brazilian official Red List ([ICMBio](#),
308 [2023](#)), DD was the most frequent category, applied to 24 (47%) species, followed by LC
309 (21.5%) and EN (7.84%). Six (11.7%) gap species were not assessed by [ICMBio](#) ([2023](#)).

310 1.3.4 *Range size, habitat loss, protection and threat levels of Cerrado endemic*
311 *tetrapods*

312 Most Cerrado endemic tetrapods are not widespread in the Cerrado, showing res-
313 tricted (49.7%) or partial (42.9%) ranges. Range sizes are significantly different among
314 Cerrado tetrapod classes (Kruskal-Wallis $\chi^2 = 31.76$, $df = 3$, $p < 0.001$), with anurans
315 and reptiles tending to show smaller ranges than mammals and birds (see [Supporting](#)
316 [information - Figure S2](#)). Two species (*Hylaeamys acritus* and *Juscelinomys huanchacae*,
317 both considered DD in the global Red List) were not assessed for land cover, as their ran-
318 ges are outside the Brazilian border, in areas lacking MapBiomas land-use classification.
319 Amongst the remaining 338 species, a total of 294 (86.98%) have lost natural habitats
320 within their range between 2000 and 2020, with an average of 8% of loss, ranging from
321 0.1% to a maximum of 45% ([Supporting information - Appendix S1](#)). Habitat loss affected
322 129 (43.87%), 140 (47.61%) and 25 (8.5%) species with restricted, partial and widespread
323 geographical ranges, respectively. On the other hand, 39 species (11.5%) showed marginal
324 gains (an average of 4.63%) in natural habitats within their ranges ([Supporting informa-](#)
325 [tion - Appendix S1](#)). Details on species range categories, natural habitat modification
326 (gain or loss), and range protection categories can be found in [Supporting information -](#)
327 [Figure S2](#).

328 A total of 265 species (77.9%) were assessed by the IUCN Red List, while 315 (92.6%)
329 were assessed in the Brazilian official Red List (both using the same IUCN categories and
330 criteria, [Figure 4](#)). Birds are, proportionally, the most threatened tetrapod class, followed
331 by mammals and reptiles, with amphibians being the least threatened in both lists (see
332 [Figure 4a](#)). Proportions of DD species in the IUCN Red List were always higher than
333 those in the Brazilian assessment. In the global IUCN Red List, the percentage of DD
334 species was higher for amphibians (43.9%), followed by reptiles (27.41%) and mammals
335 (18.91%), while in the Brazilian official Red List proportions of DD species peaked in
336 reptiles (15.65%), followed by mammals (10.81%) and amphibians (9.32%). Due to the
337 higher number of assessed species, more recent completion date and smaller proportion of
338 DD species, the following results are all based on the Brazilian official Red List ([ICMBio](#),

339 2023).

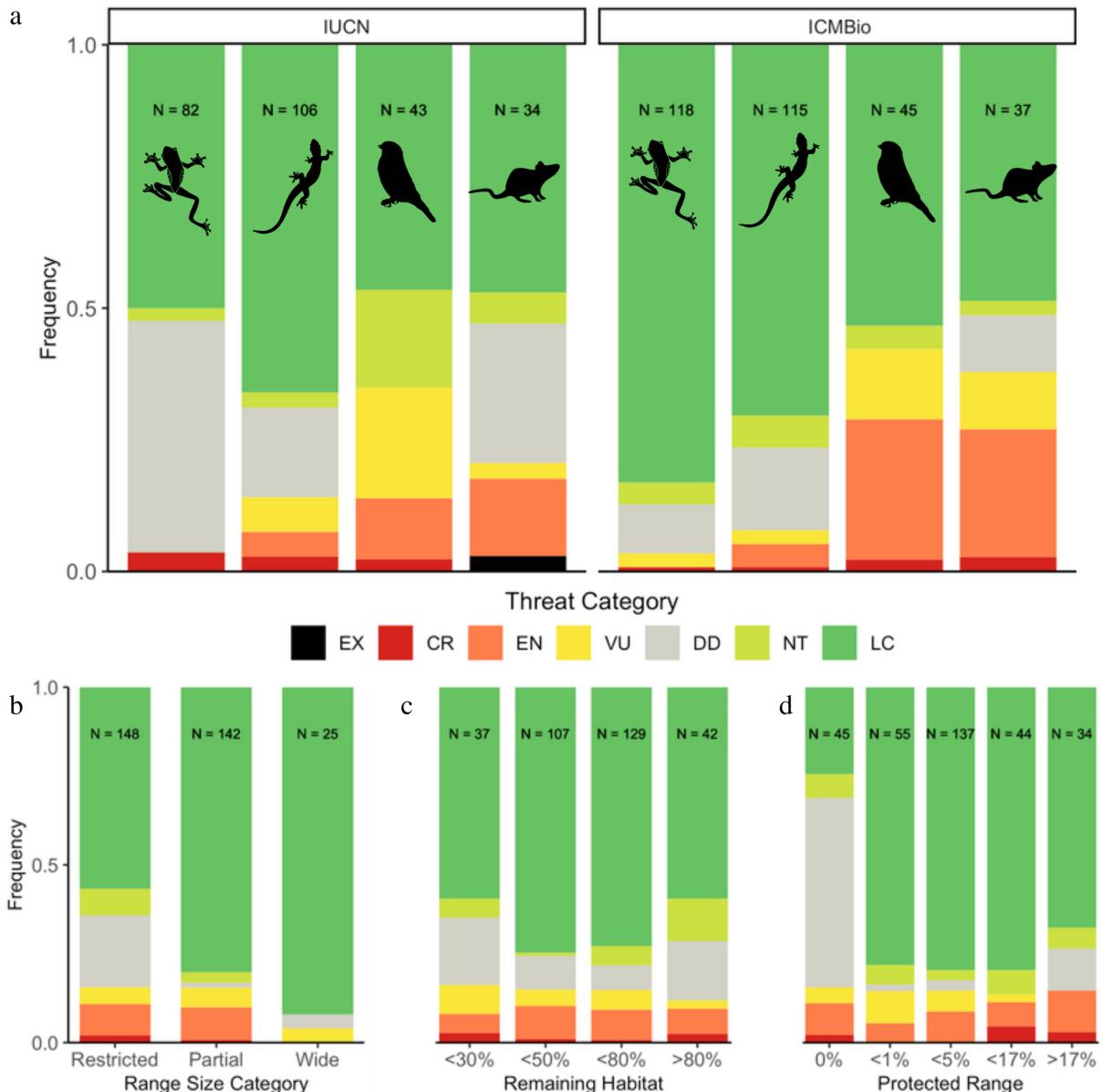


Figure 4 – Proportion and numbers of endemic tetrapod species in each IUCN category, according to the IUCN global Red List ($N = 265$) and the Brazilian official Red List ($N = 315$) (a); and according to range size (b), percentage of remaining habitat (c), and percentage of protection on PAs (IUCN categories I-IV, d). Categories in figures 4b, c and d, follow the Brazilian official Red List ($N = 315$).

340 Proportions of species in threat categories were significantly different among tetra-
 341 pod classes ($\chi^2 = 54.52$; $df = 3$; $p < 0.001$), being higher in birds (42.2%) and mammals
 342 (37.8%) than in amphibians (3.38%) and reptiles (7.82%). The proportion of threatened
 343 and DD species was higher among restricted-range or partially ranged species than in
 344 widespread taxa, the majority of which were assessed as LC (Figure 4b). Threatened and
 345 non-threatened species in the Brazilian official Red List showed no significant differences
 346 in range size (Kruskal-Wallis $\chi^2 = 0.000039$, $df = 1$; $p = 0.99$). However, range sizes were

347 significantly different if we considered all IUCN categories (Kruskal-Wallis $\chi^2 = 48.04$, df
348 = 5; $p < 0.001$), with Vulnerable birds and mammals showing large ranges, while spe-
349 cies assessed as Critically Endangered, Vulnerable amphibians, and data-deficient reptiles
350 often showing small ranges ([Supporting information - Figure S3](#)).

351 Proportions of threatened and DD species seem poorly related to levels of habitat
352 loss, although the percentage of threatened species was slightly higher in species showing
353 less than 30% remaining habitat ([Figure 4c](#)). Threatened and non-threatened (binary
354 test) species in the Brazilian official Red List showed no significant differences in the
355 percentage of remaining habitat within ranges (Kruskal-Wallis $\chi^2 = 0.33$, $df = 1$; $p =$
356 0.56). Moreover, species assigned to different threat categories (including all categories)
357 also showed no significant differences in the percentage of remaining habitat (Kruskal-
358 Wallis $\chi^2 = 5.63$, $df = 5$; $p = 0.34$; [Supporting information - Figure S4](#)).

359 Proportions of threatened and non-threatened species also seem poorly related to
360 levels of protection ([Figure 4d](#)). However, the proportion of DD species is noticeably
361 higher in gap species (see [Figure 4d](#)). Threatened and non-threatened (binary test) species
362 in the Brazilian official Red List showed no significant differences in protection within
363 ranges (Kruskal-Wallis $\chi^2 = 0.75$, $df = 1$; $p = 0.38$). However, species assigned to different
364 IUCN categories (including all categories) differed in the percentage of protection within
365 ranges (Kruskal-Wallis $\chi^2 = 36.146$, $df = 5$; $p < 0.001$), with some Least Concern species
366 showing a higher proportion of protected ranges ([Supporting information - Figure S5](#)).

367 1.3.5 Vulnerability, Irreplaceability and Discovery

368 We observed a significant negative correlation between range size and date of species
369 descriptions: recently described endemics tended to show localised, narrow ranges, while
370 species described in early taxonomic studies tended to be widespread ($F_{1, 313} = 48.19$,
371 $R^2 = 0.1334$, $p < 0.001$; [Figure 5a](#)). Threatened and non-threatened species seem scat-
372 tered among different description dates and range sizes. However, the DD category was
373 concentrated in species with recent descriptions, especially amphibians and reptiles (see
374 [Figure 5a](#)).

375 Threatened species also seem relatively scattered according to range size and pro-
376 portion of habitat loss ([Figure 5b](#)). However, many DD species (especially amphibians
377 and reptiles) showed narrow ranges (see [Figure 5b](#) and [Figure 4c](#)), including species hea-
378 vily impacted by habitat loss (see [Figure 5b](#)). Moreover, all CR species were concentrated
379 in the left portion of the graph, showing restricted ranges (see [Figure 5b](#) and [Figure 4c](#)).

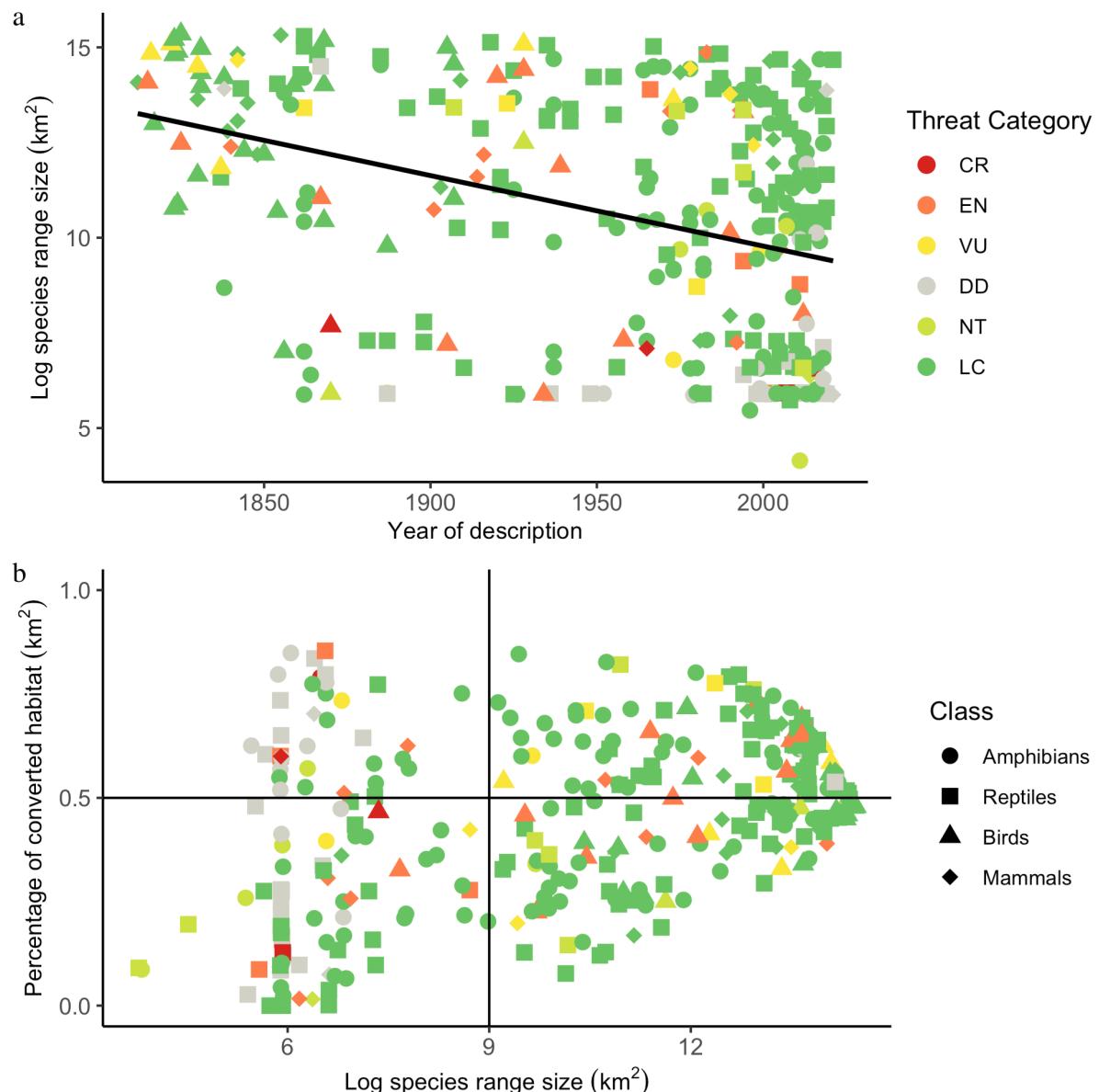


Figure 5 – Relationship between range size and date of description (a) and percentage of remaining habitat within ranges (b) of Cerrado endemic tetrapods. Symbols indicate tetrapod classes and colours indicate IUCN categories in the Brazilian official Red List (ICMBio, 2023).

380 1.4 Discussion

381 The so-called Linnean Shortfall (e.g. lack of knowledge on actual species diversity;
 382 Hortal et al., 2015) has long been claimed to preclude proper conservation planning,
 383 especially at refined scales (Whittaker et al., 2005). Knowledge on terrestrial vertebrates
 384 and the predicted diversity of the best-known animal groups on the planet (J. H. Brown,
 385 1995) proved to be highly underestimated in the Cerrado at the time of the classic hotspot
 386 paper (Myers et al., 2000). Since 2000 however, basic biodiversity knowledge in the
 387 Cerrado has improved significantly, both in quality and quantity. In fact, more than

388 one-third of all currently known endemic terrestrial vertebrate species were described
389 in the last two decades. Herein we show that both vulnerability and irreplaceability
390 levels have risen sharply in the Cerrado. Recent field efforts, directed towards sampling
391 gaps, coupled with resulting taxonomic advances, were determinant to the steep rise in
392 vertebrate diversity knowledge in the last 20 years, both in poorly known regions, like
393 northern Cerrado, as in highly sampled areas such as the Espinhaço Mountain Range, or
394 Central Brazilian plateau (Azevedo et al., 2016; Carmignotto et al., 2022; Nogueira et al.,
395 2019, 2010, 2009; Valdujo et al., 2012).

396 Our results, however, indicate that the pace of taxonomic and biogeographical dis-
397 covery in the Cerrado has not been coupled with effective conservation action on the
398 ground. The recent increase in taxonomic knowledge results in the detection of highly
399 complex, endemic and highly threatened biotas, still marginally represented in protected
400 areas and under persistent pressure of habitat loss resulting from large-scale changes in
401 land use after the expansion of the agricultural frontier in central Brazil (P. Pacheco et
402 al., 2021; see also Vieira-Alencar et al., 2023), continuing a trend already detected in the
403 late XXth century (Klink & Machado, 2005; Ratter et al., 1997). Hence, the coupled
404 increase in endemism and habitat loss results in the detection of highly vulnerable and
405 irreplaceable taxa and areas, already largely impacted by habitat loss and fragmentation
406 (Strassburg et al., 2017; Vieira-Alencar et al., 2023).

407 Our results reinforce previously detected conservation prioritizations in northern
408 Cerrado (e.g. Monteiro et al., 2020; Vieira-Alencar et al., 2023) and the urgency to take
409 action and to secure the last opportunities to safeguard the last continuous areas of
410 preserved Cerrado (Vieira-Alencar et al., 2023). However, conservation action should also
411 be directed to safeguarding the last remnants of Cerrado in southeastern Brazil, regardless
412 of their size and current connectivity, given that these highly impacted and fragmented
413 regions harbour many threatened or restricted-range Cerrado endemics, and may serve
414 as important backbones to the implementation of restoration programmes (Strassburg et
415 al., 2017; Vieira-Alencar et al., 2023).

416 A recent study on the interactions between the effects of Linnean and Wallacean
417 shortfalls on species threat (Baranzelli, Villalobos, Cordier, & Nori, 2023) indicates that
418 increased knowledge on species distribution and increased taxonomic knowledge have
419 antagonistic effects on threat perception: while a higher number of described species
420 indicate increased threats, the detection of new range data and wider distributions lead to
421 decreased threat perception. However, our results indicate that most new data on species
422 ranges result in better taxonomic resolution and the detection of smaller, local ranges,
423 and not more widespread taxa. In other words, the more we understand ranges, the more
424 species are described, either as a result of splitting previous ranges or via the detection of
425 allopatric, peripheral, isolated new taxa and populations (Azevedo et al., 2016; Nogueira
426 et al., 2011). Moreover, even new records of restricted-range endemic tetrapods from

427 the highly impacted southern Cerrado will still come from extremely small and isolated
428 fragments of Cerrado (see [Serrano et al., 2023](#)) describing very impacted populations
429 prone to extinction in the next few decades ([Strassburg et al., 2017](#)).

430 In sum, our data indicate that Cerrado endemic tetrapods, including the many re-
431 cently discovered and described restricted-range taxa, are at great risk of a severe cycle
432 of extinction in the next few decades. In fact, ca. 480 endemic Cerrado vascular plant
433 species are estimated to become extinct in the near future (until 2050) if current rates of
434 habitat loss and conversion to croplands are not urgently halted and reversed in central
435 Brazilian savannas ([Strassburg et al., 2017](#)). Even worse, at least one-third of Cerrado's
436 plant species distribution within PAs is predicted to be lost due to climate change alone,
437 considering the most optimistic scenario forecasted for 2050 and 2080 ([Velazco et al.,](#)
438 [2019](#)), with habitat loss predicted to potentially increase this effect for non-protected spe-
439 cies ranges. The highest losses are predicted to occur where the greatest species richness
440 is harboured, more specifically the central and central-eastern areas of the Cerrado, where
441 we also detected high levels of overall richness and new species descriptions ([Figure 3b,c](#)).
442 However, given that the rise in tetrapod endemism spans a wider portion of the Cerrado
443 (see [Figure 3c](#)), exceeding areas of plant extinctions hotspots, we argue that the figures
444 for Cerrado tetrapods will be even more sombre than that detected for vascular plants.
445 As an example, areas such as the southern portion of the Serra Geral plateau, with high
446 rates of discovery in Cerrado tetrapods and harbouring recently described species that
447 have lost more than 40% of their known ranges (e.g. *Amphisbaena persephone*, *Amphis-*
448 *baena carli*, see [Supporting information - Appendix S1](#)) were not targeted as an area of
449 future extinctions or as a priority area for Cerrado restoration ([Strassburg et al., 2017](#)).

450 Moreover, given the high structural heterogeneity of Cerrado habitats, ranging from
451 open grasslands to wetlands and dense woodlands and forests and the noticeable habitat
452 specialisation of many Cerrado species (see [Nogueira et al., 2009, 2011](#); [Silva & Bates,](#)
453 [2002](#)), habitat requirements of Cerrado tetrapods should be a major element in guiding
454 restoration and habitat protection. As an example, restoring arboreal vegetation in areas
455 originally dominated by fire-prone grasslands may be inefficient and even deleterious to
456 grassland specialists. Both the protection and restoration of the Cerrado habitat must
457 be directed to preserving the original habitat mosaic that typifies the domain of central
458 Brazilian savannas (see [Silva & Bates, 2002](#)). The conservation of Cerrado endemic tetra-
459 pods depends both on the small or currently disconnected fragments (such as those in the
460 Southern Cerrado) as on the larger connected northern Cerrado areas. Protecting and
461 halting deforestation in both these land use scenarios is mandatory to avoid extinction
462 and collapse of Cerrado biological diversity in the coming decades ([Vieira-Alencar et al.,](#)
463 [2023](#)).

464 The recent accumulation of taxonomic and biogeographical knowledge in the Cer-
465 rado also seems poorly reflected in species threat assessments. Despite the very important

advances in biodiversity assessments worldwide and specifically in Brazil (12,254 species assessed in the last two decades, an unparalleled effort worldwide; [ICMBio, 2018](#)), many recently described, restricted-range species are still classified as DD in official Red Lists (either national or global) or have not been assessed yet. This large number of unassessed and DD species may explain the low proportions of threatened species of Cerrado anurans and reptiles. These low proportions of threatened species are not compatible with expected values based on the proportion of threatened species in the global Red List (40.7% in amphibians; 21.1% in reptiles, see [Borgelt et al., 2022](#); [N. Cox et al., 2022](#)). If the proportion of threatened Cerrado amphibians and reptiles followed the proportions on the global Red List, we would have 48 threatened amphibians and 24 reptiles in the list of threatened Cerrado endemic tetrapods. However, in the most recent and complete assessment (the Brazilian Official Red List, [ICMBio, 2023](#)), only four amphibians and nine reptiles were classified as threatened, in apparently highly underestimated figures.

Moreover, the proportions of threatened species among tetrapod classes in the Cerrado are highly heterogeneous. In contrast, global data indicate that for most (87%) terrestrial regions no tetrapod class is disproportionately threatened compared with the other classes ([N. Cox et al., 2022](#)). Hence, our results in the Cerrado disagree with a global trend of high geographical concordance of threat levels in all four tetrapod classes. On the contrary, our results show that species of amphibians and reptiles show much lower proportions of threatened species than Cerrado birds and mammals, resulting in underestimated lists of threatened Cerrado tetrapods.

A recent study, using models that suggest Red List categories or probabilities of threat for DD species concluded that 85% of amphibians, 59% of reptiles and 61% of mammals currently assessed as DD could be reassessed in a threat category (VU, EN or CR), based on the available threat and range data (see [Borgelt et al., 2022](#)). Applying these proportions to our numbers of DD species would result in the addition of 22 species (+6%) to the list of threatened Cerrado tetrapods, including nine amphibians, 11 reptiles and two mammals. Also alarming is the number of species not even assessed regarding their threat status. If the 25 described endemics species absent from the Brazilian Red List were to be assessed in a threat category using the same predictions estimated for DD species ([Borgelt et al., 2022](#)), another 16 species (five amphibians, eight reptiles and three mammals) would be included in the final threatened Cerrado endemic tetrapods species list. These combined comparisons indicate that, despite the clear advances in biodiversity documentation (species discoveries, new inventories, improved knowledge on ranges and endemism), the number of threatened tetrapod species is still grossly underestimated in the Cerrado.

We see little biological meaning in the fact that so few Cerrado amphibians and reptiles are assessed as threatened compared to birds and mammals. Given the tendency for amphibians and reptiles to show relatively restricted ranges (see [Figure S3](#) for range

size variation in each class) and much smaller dispersal capacity, species of the herpetofauna are intrinsically more prone to extinction than birds and mammals, even if only by stochasticity (Gaston, 1998; Meiri et al., 2018). A recently developed machine learning-based automated extinction risk assessment method might be useful to offer provisional assessment for the high number of non-assessed amphibians and reptiles (Caetano et al., 2022), at least to raise a red flag demanding careful validation in further specialist-based assessments. Moreover, we also fail to see biological meaning in the fact that endemic species from a highly impacted biodiversity hotspot should show lower threat levels than the global average for the same tetrapod class. Accordingly, Cerrado birds and mammals show higher proportions of threatened species when compared to the average global portions in each particular group (see N. Cox et al., 2022). In fact, birds and mammals are the best-studied vertebrate groups, especially regarding their geographical distributions and overall spatial patterns (J. H. Brown, 1995). This is reflected in extinction risk assessments which are traditionally more representative of these groups (N. Cox et al., 2022) and reinforces the need for a better understanding of the Cerrado herpetofauna and a change in paradigm amongst Brazilian herpetofauna assessment specialists.

Another special concern is the high number of restricted range, recently described endemic tetrapods detected as gap species or very poorly covered by protected areas. The lack of representation of restricted-range species was already detected for Odonates in the central portion of the Cerrado (Nóbrega & Marco, 2011), indicating that protection of Cerrado areas is not planned according to rarity or endemism patterns, but instead may be based on opportunism and the inclusion of residual areas, not targeted by economical activities (Margules & Pressey, 2000). A recent study on the threats and opportunities for the conservation of biodiversity in Madagascar, another global hotspot, indicates that the local network of PAs fails to represent only less than 3% of vertebrates with known ranges, a much lower proportion of gap species than that in our results for Cerrado tetrapods. Not surprisingly, the least protected ecoregion in Madagascar are open areas dominated by grassland-woodland mosaics, indicating that bias against open areas may at least partially explain the lack of protection of the Cerrado, the single savanna region among the 35 global hotspots (Zachos & Habel, 2011).

Endemic tetrapod richness in the largest Cerrado PAs highlights areas with the potential to trigger KBA status (KBA Standards and Appeals Committee of IUCN SSC/WCPA, 2022). Worryingly, the four richest PAs are located in the highly impacted central and southern Cerrado (Figure 3f), and the largest amongst them covers little more than 0.1% of the ecoregion. Expanding these PAs may benefit a high number of species, especially PN Chapada dos Veadeiros and PN das Emas (see Vieira-Alencar et al., 2023). Creating benefits for landowners committed to the restoration and maintenance of set-aside reserves has been hypothesised as a mandatory strategy to safeguard Cerrado biodiversity (Machado & Aguiar, 2023), as privately owned natural remnants

544 in the Cerrado have been claimed to protect up to 25% of threatened vertebrate species
545 ranges if their whole area were to be restored to suitable conditions (De Marco Jr. et al.,
546 2023). The need for restoration of southern Cerrado to secure biodiversity conservation
547 is not a novelty (see Strassburg et al., 2017; Vieira-Alencar et al., 2023), however, these
548 recent findings (De Marco Jr. et al., 2023) open a promising avenue of conservation invest-
549 ment that involves the government, non-government organisations, the private sector and
550 the social community (Machado & Aguiar, 2023). Moreover, despite not being strictly
551 designated for conserving biodiversity (therefore not being included in analyses as PAs;
552 Locke & Dearden, 2005), it has been shown that indigenous lands are capable of halting
553 deforestation as much as PAs (Sze, Carrasco, Childs, & Edwards, 2022), and should be
554 considered as an alternative, meeting both the environmental and social agendas with
555 lower costs.

556 Overall, our data indicate that lack of basic information on species diversity, dis-
557 tribution and endemism, pervasive in the Neotropics and in most megadiverse regions of
558 the planet, should no longer be pointed as an impediment to effective conservation action
559 in the Cerrado. Knowledge on endemism and diversity of Cerrado faunas has improved
560 quickly in recent decades, and the conservation of the species and areas highlighted here
561 will certainly represent a significant improvement for safeguarding Neotropical and global
562 biodiversity. Meanwhile, time for urgent and decisive conservation action in the Cerrado
563 is quickly running out, and the next decade represents the last chance to conserve the
564 unique, complex and most diverse tropical savannas in the globe.

565 1.5 Supporting information

566 Appendix S1

Appendix Table 1: Summary of compiled information on Cerrado's endemic terrestrial vertebrate species, including: Class (Taxa: Amp - Amphibians; Rep - Reptiles; Birds and Mam - Mammals), binomial (Species), year of description (Year), extinction risk category according to the global (IUCN), and Brazilian (ICMBio) assessments, total range size (T.Range), range size category (Category), range size within the Cerrado's limits as proposed by [Dinerstein et al., 2017](#) (C.Range), area (in km²) of natural habitat within the species range in 2000 (Nat2000), and 2020 (Nat2020), percentage of remaining natural habitat in 2020 in relation to range size (PercNat), habitat loss between 2000 and 2020 (Loss), percentage of habitat lost between 2000 and 2020 in relation to range size (PercLoss), area (in km²) of the species total range within strict protection PAs (ProtRange), and percentage of species protected range in relation to total range size (PercProt). All measures of remaining habitat and habitat loss were calculated in relation to a species range size within the Cerrado's limits as proposed by [Dinerstein et al., 2017](#) (C.Range).

Groups	Species	Year	IUCN	ICMBio	T.Range	Category	C.Range	Nat2000	Nat2020	PercNat	Loss	PercLoss	ProtRange	PercProt
Amp	<i>Adenomera crotuba</i>	2013	-	LC	206241	P	186835	128349	112972	0.605	15377	0.120	3399	0.017
Amp	<i>Adenomera saci</i>	2013	-	LC	731210	P	656762	411612	371462	0.566	40150	0.098	29189	0.040
Amp	<i>Allobates brunneus</i>	1887	LC	NT	373	R	373	240	229	0.614	11	0.046	0	0.000
Amp	<i>Allobates goianus</i>	1975	DD	NT	16216	R	16162	11267	10651	0.659	616	0.055	312	0.019
Amp	<i>Ameerega berohoka</i>	2011	LC	LC	110480	P	105972	46535	41319	0.390	5216	0.112	669	0.006
Amp	<i>Ameerega braccata</i>	1864	LC	LC	600	R	600	469	474	0.790	-5	-0.011	133	0.222
Amp	<i>Ameerega flavopicta</i>	1925	LC	LC	868222	P	544212	307455	279326	0.513	28129	0.091	18023	0.021
Amp	<i>Ameerega picta</i>	1838	LC	LC	5921	R	3951	2362	2283	0.578	79	0.033	397	0.067
Amp	<i>Aplastodiscus lutzorum</i>	2017	-	LC	20219	R	20269	11365	10643	0.525	722	0.064	703	0.035
Amp	<i>Barycholos ternetzi</i>	1937	LC	LC	724474	P	649288	370547	334957	0.516	35590	0.096	22695	0.031
Amp	<i>Boana botumirim</i>	2009	-	LC	364	R	365	352	349	0.956	3	0.009	121	0.332
Amp	<i>Boana buriti</i>	1999	DD	VU	15413	R	15402	6765	6138	0.399	627	0.093	43	0.003
Amp	<i>Boana caiapo</i>	2018	-	LC	262878	R	186822	126058	113969	0.610	12089	0.096	9377	0.036
Amp	<i>Boana cipoensis</i>	1968	NT	LC	7857	R	5613	4610	4393	0.783	217	0.047	374	0.048
Amp	<i>Boana ericae</i>	2000	DD	LC	963	R	964	905	901	0.935	4	0.004	197	0.205
Amp	<i>Boana goiana</i>	1968	LC	LC	35423	R	35488	18218	16960	0.478	1258	0.069	731	0.021
Amp	<i>Boana jaguariaivensis</i>	2010	-	LC	1041	R	525	217	249	0.474	-32	-0.147	2	0.002

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Groups	Species	Year	IUCN	ICMBio	T.Range	Category	C.Range	Nat2000	Nat2020	PercNat	Loss	PercLoss	ProtRange	PercProt	Capítulo 1. Hotspot getting hotter
Amp	<i>Boana lundii</i>	1856	LC	LC	988264	P	814835	337416	311550	0.382	25866	0.077	13841	0.014	
Amp	<i>Boana stenocephala</i>	1999	DD	LC	712	R	712	162	177	0.249	-15	-0.093	0	0.000	
Amp	<i>Bokermannohyla alvarengai</i>	1956	LC	LC	28510	R	18393	14447	13590	0.739	857	0.059	1510	0.053	
Amp	<i>Bokermannohyla ibitiguara</i>	1983	DD	LC	1499	R	1496	678	695	0.465	-17	-0.025	891	0.594	
Amp	<i>Bokermannohyla izecksohni</i>	1979	CR	DD	351	R	350	69	71	0.203	-2	-0.029	0	0.000	
Amp	<i>Bokermannohyla nanuzae</i>	1973	LC	LC	9366	R	3183	2080	2061	0.648	19	0.009	552	0.059	
Amp	<i>Bokermannohyla napolii</i>	2012	-	VU	904	R	903	259	240	0.266	19	0.073	0	0.000	
Amp	<i>Bokermannohyla pseudopseudis</i>	1937	LC	LC	19647	P	19642	15829	15047	0.766	782	0.049	2069	0.105	
Amp	<i>Bokermannohyla ravidai</i>	2001	DD	DD	361	R	362	160	156	0.431	4	0.025	0	0.000	
Amp	<i>Bokermannohyla sagarana</i>	2011	NT	NT	63	R	46	43	42	0.913	1	0.023	3	0.048	
Amp	<i>Bokermannohyla sapiranga</i>	2012	-	LC	32737	R	32680	13721	11913	0.365	1808	0.132	497	0.015	
Amp	<i>Bokermannohyla saxicola</i>	1964	LC	LC	33627	R	23195	18429	17381	0.749	1048	0.057	2731	0.081	
Amp	<i>Bokermannohyla sazimai</i>	1982	DD	LC	9364	R	9243	2431	2499	0.270	-68	-0.028	66	0.007	
Amp	<i>Chiasmocleis albopunctata</i>	1885	LC	LC	2062226	W	1459992	751051	675047	0.462	76004	0.101	41764	0.020	
Amp	<i>Chiasmocleis centralis</i>	1952	DD	DD	368	P	369	190	149	0.404	41	0.216	0	0.000	
Amp	<i>Crossodactylus franciscanus</i>	2015	-	CR	714	R	657	137	138	0.210	-1	-0.007	91	0.128	
Amp	<i>Crossodactylus trachystomus</i>	1862	DD	LC	33530	R	19915	13959	13244	0.665	715	0.051	2490	0.074	
Amp	<i>Dendropsophus anataliasiasi</i>	1972	LC	LC	400550	P	307871	214093	190107	0.618	23986	0.112	10619	0.027	
Amp	<i>Dendropsophus araguaya</i>	1998	DD	LC	2451	R	2451	1142	1052	0.429	90	0.079	0	0.000	
Amp	<i>Dendropsophus cerradensis</i>	1998	DD	DD	714	R	716	166	159	0.222	7	0.042	0	0.000	
Amp	<i>Dendropsophus cruzi</i>	1998	LC	LC	944655	P	731668	431582	388771	0.531	42811	0.099	25152	0.027	
Amp	<i>Dendropsophus elianeae</i>	2000	LC	LC	980367	P	719787	218925	203858	0.283	15067	0.069	6428	0.007	
Amp	<i>Dendropsophus jimi</i>	1999	LC	LC	828098	P	554987	149135	141123	0.254	8012	0.054	4985	0.006	
Amp	<i>Dendropsophus rhea</i>	1999	DD	DD	420	R	423	59	64	0.151	-5	-0.085	0	0.000	
Amp	<i>Dendropsophus rubicundulus</i>	1862	LC	LC	1479361	P	1115651	705618	635401	0.570	70217	0.100	44925	0.030	
Amp	<i>Dendropsophus tritaeniatus</i>	1965	LC	LC	1460	R	1461	673	610	0.418	63	0.094	75	0.051	
Amp	<i>Elachistocleis bumbameuboi</i>	2010	DD	LC	757	R	377	323	251	0.666	72	0.223	0	0.000	
Amp	<i>Elachistocleis matogrossensis</i>	2010	LC	LC	158207	P	55528	28656	25882	0.466	2774	0.097	1085	0.007	
Amp	<i>Hyloides otavioi</i>	1983	DD	NT	375	R	216	159	160	0.741	-1	-0.006	74	0.197	
Amp	<i>Ischnocnema penaxavantinho</i>	2007	DD	LC	45228	R	44081	14682	13259	0.301	1423	0.097	55	0.001	
Amp	<i>Leptodactylus brevipes</i>	1887	-	-	207024	P	165495	94928	80886	0.489	14042	0.148	568	0.003	
Amp	<i>Leptodactylus camaquara</i>	1978	DD	LC	12495	R	7967	6725	6352	0.797	373	0.055	892	0.071	
Amp	<i>Leptodactylus cunicularius</i>	1978	LC	LC	42533	R	18512	5859	5927	0.320	-68	-0.012	494	0.012	
Amp	<i>Leptodactylus furnarius</i>	1978	LC	LC	1856186	P	1305612	648092	585617	0.449	62475	0.096	28313	0.015	
Amp	<i>Leptodactylus kilombo</i>	2020	-	-	32359	R	28996	20589	15893	0.548	4696	0.228	601	0.019	
Amp	<i>Leptodactylus pustulatus</i>	1970	LC	LC	1805011	P	946770	696634	612020	0.646	84614	0.121	39705	0.022	

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Groups	Species	Year	IUCN	ICMBio	T.Range	Category	C.Range	Nat2000	Nat2020	PercNat	Loss	PercLoss	ProtRange	PercProt	Capítulo 1. Hotspot getting hotter
Amp	<i>Leptodactylus sertanejo</i>	2007	LC	LC	1955949	W	1463510	765103	686055	0.469	79048	0.103	41134	0.021	
Amp	<i>Leptodactylus tapiti</i>	1978	DD	LC	369	R	370	335	332	0.897	3	0.009	73	0.198	
Amp	<i>Lysapsus caraya</i>	1964	LC	LC	36218	R	32573	28711	27590	0.847	1121	0.039	7269	0.201	
Amp	<i>Odontophrynus cultripes</i>	1862	LC	LC	602779	P	469728	152655	144132	0.307	8523	0.056	5950	0.010	
Amp	<i>Odontophrynus juquinha</i>	2017	-	LC	43994	R	26800	19956	18769	0.700	1187	0.059	3026	0.069	
Amp	<i>Odontophrynus monachus</i>	2012	-	LC	358	R	357	154	161	0.451	-7	-0.045	186	0.520	
Amp	<i>Oreobates antrum</i>	2018	-	LC	1286	R	1285	817	763	0.594	54	0.066	24	0.019	
Amp	<i>Oreobates heterodactylus</i>	1937	DD	LC	16557	R	16534	11872	10771	0.651	1101	0.093	524	0.032	
Amp	<i>Oreobates remotus</i>	2012	-	LC	933	R	932	806	775	0.832	31	0.038	389	0.417	
Amp	<i>Phasmahyla jandaia</i>	1978	LC	LC	11924	R	3699	2469	2359	0.638	110	0.045	425	0.036	
Amp	<i>Physalaemus atim</i>	2015	-	LC	583	R	584	131	132	0.226	-1	-0.008	5	0.009	
Amp	<i>Physalaemus centralis</i>	1962	LC	LC	1826841	W	1249096	663858	596555	0.478	67303	0.101	39992	0.022	
Amp	<i>Physalaemus claptoni</i>	2020	-	-	360	R	361	305	304	0.842	1	0.003	57	0.158	
Amp	<i>Physalaemus deimaticus</i>	1988	DD	LC	2352	R	2350	1859	1831	0.779	28	0.015	104	0.044	
Amp	<i>Physalaemus evangelistai</i>	1967	DD	LC	5445	R	5447	3955	3874	0.711	81	0.020	474	0.087	
Amp	<i>Physalaemus marmoratus</i>	1862	LC	LC	1228199	P	935891	368155	337897	0.361	30258	0.082	16089	0.013	
Amp	<i>Physalaemus nattereri</i>	1863	LC	LC	1987481	W	1424770	741061	663446	0.466	77615	0.105	41283	0.021	
Amp	<i>Pithecopus araguaius</i>	2017	-	LC	1108	P	1108	665	656	0.592	9	0.014	98	0.088	
Amp	<i>Pithecopus ayeaye</i>	1966	CR	LC	72110	P	29528	8684	8897	0.301	-213	-0.025	2091	0.029	
Amp	<i>Pithecopus azureus</i>	1862	DD	LC	2392121	P	1597277	950984	849310	0.532	101674	0.107	53593	0.022	
Amp	<i>Pithecopus centralis</i>	1965	DD	LC	105166	P	63707	33301	30253	0.475	3048	0.092	581	0.006	
Amp	<i>Pithecopus megacephalus</i>	1926	DD	LC	53181	R	30727	21335	20157	0.656	1178	0.055	3718	0.070	
Amp	<i>Pithecopus oreades</i>	2002	DD	LC	82568	P	82606	40787	37135	0.450	3652	0.090	1701	0.021	
Amp	<i>Pristimantis dundeei</i>	1999	DD	LC	113765	P	112363	44955	40964	0.365	3991	0.089	1843	0.016	
Amp	<i>Pristimantis moa</i>	2020	-	-	29032	R	27224	25107	21542	0.791	3565	0.142	380	0.013	
Amp	<i>Pristimantis ventrigranulosus</i>	2012	-	LC	13038	R	13019	5499	4628	0.356	871	0.158	0	0.000	
Amp	<i>Proceratophrys bagnoi</i>	2013	-	DD	926	R	925	787	728	0.787	59	0.075	0	0.000	
Amp	<i>Proceratophrys branti</i>	2013	-	LC	151905	P	145958	119772	108842	0.746	10930	0.091	12781	0.084	
Amp	<i>Proceratophrys carranca</i>	2013	-	DD	363	R	362	178	174	0.481	4	0.022	0	0.000	
Amp	<i>Proceratophrys cururu</i>	1998	DD	LC	2291	R	2297	1840	1813	0.789	27	0.015	426	0.186	
Amp	<i>Proceratophrys dibernardoi</i>	2013	-	LC	66603	P	66552	20815	19043	0.286	1772	0.085	1647	0.025	
Amp	<i>Proceratophrys goyana</i>	1937	LC	LC	100782	P	99403	65281	60672	0.610	4609	0.071	2507	0.025	
Amp	<i>Proceratophrys huntingtoni</i>	2012	-	LC	1102	R	926	759	694	0.750	65	0.086	0	0.000	
Amp	<i>Proceratophrys moratoi</i>	1980	CR	LC	226403	P	175424	35509	34847	0.199	662	0.019	1027	0.005	
Amp	<i>Proceratophrys rotundipalpebra</i>	2013	-	LC	376	R	378	366	369	0.976	-3	-0.008	252	0.670	
Amp	<i>Proceratophrys salvatori</i>	1996	DD	LC	28016	R	28058	14359	13201	0.471	1158	0.081	731	0.026	

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Amp	<i>Proceratophrys strussmannae</i>	2011	-	DD	236	R	235	86	88	0.375	-2	-0.023	0	0.000	
Amp	<i>Proceratophrys vielliardi</i>	2011	DD	LC	21126	R	21170	9080	7578	0.358	1502	0.165	242	0.012	
Amp	<i>Pseudis tocantins</i>	1998	LC	LC	304291	P	252204	190485	170652	0.677	19833	0.104	11099	0.037	
Amp	<i>Pseudopaludicola atragula</i>	2014	-	LC	12616	R	12570	1764	1934	0.154	-170	-0.096	0	0.000	
Amp	<i>Pseudopaludicola coracoralinae</i>	2020	-	-	731	R	730	117	125	0.171	-8	-0.068	0	0.000	
Amp	<i>Pseudopaludicola facureae</i>	2013	-	LC	64702	P	46359	8199	8031	0.173	168	0.020	158	0.002	
Amp	<i>Pseudopaludicola ibisoroca</i>	2016	-	LC	726	R	726	235	227	0.313	8	0.034	0	0.000	
Amp	<i>Pseudopaludicola jazmynmcdonaldae</i>	2019	-	-	409	R	409	301	308	0.753	-7	-0.023	184	0.450	
Amp	<i>Pseudopaludicola mineira</i>	1994	DD	LC	722	R	721	607	611	0.847	-4	-0.007	364	0.504	
Amp	<i>Pseudopaludicola ternetzi</i>	1937	LC	LC	1068878	P	868243	414362	374343	0.431	40019	0.097	15763	0.015	
Amp	<i>Rhinella cerradensis</i>	2007	DD	LC	611704	P	567519	266877	234780	0.414	32097	0.120	12574	0.021	
Amp	<i>Rhinella inopina</i>	2012	-	LC	54769	R	53160	46643	39536	0.744	7107	0.152	2607	0.048	
Amp	<i>Rhinella ocellata</i>	1858	LC	LC	1659819	P	1005633	618775	554090	0.551	64685	0.105	31130	0.019	
Amp	<i>Rhinella rubescens</i>	1925	LC	LC	724425	P	548427	229793	214622	0.391	15171	0.066	13409	0.019	
Amp	<i>Rhinella scitula</i>	2003	DD	LC	77788	P	50939	20267	18517	0.364	1750	0.086	1865	0.024	
Amp	<i>Rhinella sebbeni</i>	2015	-	LC	14562	R	13076	5546	5229	0.400	317	0.057	8	0.001	
Amp	<i>Rhinella veredas</i>	2007	LC	LC	86363	P	83024	70544	62986	0.759	7558	0.107	3609	0.042	
Amp	<i>Scinax cabralensis</i>	2007	DD	NT	725	R	543	253	233	0.429	20	0.079	45	0.062	
Amp	<i>Scinax canastrensis</i>	1982	DD	LC	29866	R	29388	8343	8512	0.290	-169	-0.020	1994	0.067	
Amp	<i>Scinax centralis</i>	1996	LC	LC	11094	R	11088	3710	3407	0.307	303	0.082	48	0.004	
Amp	<i>Scinax constrictus</i>	2005	LC	LC	1067899	P	701536	427315	380611	0.543	46704	0.109	16491	0.015	
Amp	<i>Scinax curicica</i>	2004	DD	LC	19813	R	19747	14886	14143	0.716	743	0.050	1093	0.055	
Amp	<i>Scinax goya</i>	2018	-	DD	368	R	368	267	216	0.587	51	0.191	0	0.000	
Amp	<i>Scinax haddadorum</i>	2016	-	DD	541	R	541	211	203	0.375	8	0.038	20	0.037	
Amp	<i>Scinax machadoi</i>	1973	LC	LC	25000	R	15322	12444	11841	0.773	603	0.048	1876	0.075	
Amp	<i>Scinax maracaya</i>	1980	DD	LC	9703	R	5392	1287	1340	0.249	-53	-0.041	278	0.029	
Amp	<i>Scinax pinimus</i>	1973	DD	VU	719	R	717	433	433	0.604	0	0.000	2	0.003	
Amp	<i>Scinax pombali</i>	2013	-	DD	891	R	891	453	469	0.526	-16	-0.035	564	0.633	
Amp	<i>Scinax rogerioi</i>	2009	-	LC	153012	P	145327	58511	54074	0.372	4437	0.076	484	0.003	
Amp	<i>Scinax rossaferesae</i>	2016	-	LC	4627	R	2240	812	910	0.406	-98	-0.121	174	0.038	
Amp	<i>Scinax rupestris</i>	2015	-	LC	816	R	816	760	758	0.929	2	0.003	199	0.244	
Amp	<i>Scinax skaios</i>	2010	-	LC	38789	R	38793	21067	19687	0.508	1380	0.066	744	0.019	
Amp	<i>Scinax tigrinus</i>	2010	LC	LC	44500	R	44316	19768	17687	0.399	2081	0.105	603	0.014	
Amp	<i>Thoropa megatypanum</i>	1984	LC	LC	35245	R	22801	16636	15831	0.694	805	0.048	2766	0.079	
Amp	<i>Trachycephalus mambaiensis</i>	2009	-	LC	81510	P	75730	62267	54604	0.721	7663	0.123	4752	0.058	
Rep	<i>Alopoglossus collii</i>	2020	-	-	1112	R	1112	576	552	0.496	24	0.042	0	0.000	

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Rep	<i>Ameiva jacuba</i>	2013	-	-	1264	R	1264	916	861	0.681	55	0.060	570	0.451	
Rep	<i>Ameiva parecis</i>	2003	VU	EN	372	R	371	338	312	0.841	26	0.077	0	0.000	
Rep	<i>Ameivula cipoensis</i>	2014	-	-	1157	R	675	515	521	0.772	-6	-0.012	246	0.213	
Rep	<i>Ameivula jalapensis</i>	2009	LC	LC	745	R	744	744	743	0.999	1	0.001	98	0.132	
Rep	<i>Ameivula mumbuca</i>	2003	LC	LC	747	R	746	727	718	0.963	9	0.012	130	0.174	
Rep	<i>Ameivula xaciabi</i>	2014	-	LC	42875	R	42046	40120	36962	0.879	3158	0.079	4082	0.095	
Rep	<i>Amphisbaena absaberi</i>	2001	DD	DD	366	R	291	162	115	0.395	47	0.290	0	0.000	
Rep	<i>Amphisbaena acrobelos</i>	2009	LC	LC	374	R	375	374	375	1.000	-1	-0.003	140	0.374	
Rep	<i>Amphisbaena anaemariae</i>	1997	LC	LC	346771	P	284235	92464	84609	0.298	7855	0.085	1397	0.004	
Rep	<i>Amphisbaena bedai</i>	1991	LC	LC	1543	R	1544	419	351	0.227	68	0.162	0	0.000	
Rep	<i>Amphisbaena brevis</i>	2009	DD	DD	368	R	366	292	287	0.784	5	0.017	0	0.000	
Rep	<i>Amphisbaena carli</i>	2010	LC	LC	1478	R	1478	1340	734	0.497	606	0.452	59	0.040	
Rep	<i>Amphisbaena crisae</i>	1997	DD	LC	1479	P	1432	1235	1205	0.842	30	0.024	328	0.222	
Rep	<i>Amphisbaena cuiabana</i>	2001	LC	LC	30163	R	13764	9022	7893	0.574	1129	0.125	201	0.007	
Rep	<i>Amphisbaena filiformis</i>	2016	-	DD	755	R	680	506	451	0.663	55	0.109	0	0.000	
Rep	<i>Amphisbaena kraoh</i>	1971	LC	LC	14095	R	13675	12895	11923	0.872	972	0.075	1531	0.109	
Rep	<i>Amphisbaena leeseri</i>	1964	LC	LC	141174	R	109322	35072	31608	0.289	3464	0.099	990	0.007	
Rep	<i>Amphisbaena maranhensis</i>	2012	DD	DD	377	R	378	349	332	0.878	17	0.049	0	0.000	
Rep	<i>Amphisbaena mebengokre</i>	2019	-	DD	365	R	366	136	128	0.350	8	0.059	0	0.000	
Rep	<i>Amphisbaena neglecta</i>	1936	DD	DD	367	R	366	275	274	0.749	1	0.004	5	0.014	
Rep	<i>Amphisbaena persephone</i>	2014	-	-	370	R	369	370	207	0.561	163	0.441	0	0.000	
Rep	<i>Amphisbaena sanctaeritae</i>	1994	CR	DD	602	R	602	91	99	0.165	-8	-0.088	8	0.013	
Rep	<i>Amphisbaena saxosa</i>	2003	NT	NT	375	R	44	41	40	0.909	1	0.024	0	0.000	
Rep	<i>Amphisbaena silvestrii</i>	1902	LC	LC	895546	P	432222	260313	231363	0.535	28950	0.111	9471	0.011	
Rep	<i>Amphisbaena steindachneri</i>	1881	LC	LC	1477	R	283	210	205	0.724	5	0.024	153	0.104	
Rep	<i>Amphisbaena talisiae</i>	1995	LC	LC	103006	P	91092	41840	38538	0.423	3302	0.079	1314	0.013	
Rep	<i>Anolis meridionalis</i>	1885	LC	LC	2579006	W	1407833	715321	639976	0.455	75345	0.105	58501	0.023	
Rep	<i>Apostolepis adhara</i>	2018	-	DD	371	R	371	277	309	0.833	-32	-0.116	0	0.000	
Rep	<i>Apostolepis albicularis</i>	2002	LC	LC	52589	R	48549	20060	18549	0.382	1511	0.075	651	0.012	
Rep	<i>Apostolepis assimilis</i>	1861	LC	LC	1601004	P	896267	313465	291905	0.326	21560	0.069	12789	0.008	
Rep	<i>Apostolepis barrioi</i>	1978	-	-	535264	P	227362	42693	41757	0.184	936	0.022	405	0.001	
Rep	<i>Apostolepis cerradoensis</i>	2003	DD	-	370	R	371	336	315	0.849	21	0.063	0	0.000	
Rep	<i>Apostolepis christineae</i>	2002	DD	LC	367	R	367	310	297	0.809	13	0.042	134	0.365	
Rep	<i>Apostolepis flavorotquata</i>	1854	LC	LC	1256330	P	939780	484969	437609	0.466	47360	0.098	23339	0.019	
Rep	<i>Apostolepis goiasensis</i>	1942	LC	LC	470835	P	396621	144119	133385	0.336	10734	0.074	5366	0.011	
Rep	<i>Apostolepis intermedia</i>	1898	LC	LC	1425	P	1029	540	524	0.509	16	0.030	330	0.232	

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Rep	<i>Apostolepis kikoi</i>	2018	-	DD	1240	R	1240	442	441	0.356	1	0.002	0	0.000	
Rep	<i>Apostolepis lineata</i>	1887	DD	DD	367	R	365	266	263	0.721	3	0.011	0	0.000	
Rep	<i>Apostolepis longicaudata</i>	1921	LC	LC	27040	R	25329	24615	23371	0.923	1244	0.051	2496	0.092	
Rep	<i>Apostolepis nelsonjorgei</i>	2004	LC	LC	73372	P	55799	47160	42189	0.756	4971	0.105	2925	0.040	
Rep	<i>Apostolepis phillipsae</i>	1999	VU	-	736	R	428	281	237	0.554	44	0.157	393	0.534	
Rep	<i>Apostolepis polylepis</i>	1921	LC	LC	108297	P	104924	98432	85168	0.812	13264	0.135	13842	0.128	
Rep	<i>Apostolepis sanctaeritae</i>	2005	-	LC	673293	P	614619	384081	343056	0.558	41025	0.107	21821	0.032	
Rep	<i>Apostolepis serrana</i>	2006	EN	DD	371	R	250	154	130	0.520	24	0.156	0	0.000	
Rep	<i>Apostolepis striata</i>	2004	CR	EN	371	R	363	172	145	0.399	27	0.157	0	0.000	
Rep	<i>Apostolepis tertulianobœui</i>	2004	LC	LC	1453	P	1101	636	622	0.565	14	0.022	0	0.000	
Rep	<i>Apostolepis vittata</i>	1887	VU	LC	1474	R	1353	1019	980	0.724	39	0.038	12	0.008	
Rep	<i>Atractus albuquerquei</i>	1983	LC	LC	2711519	P	945882	519934	464376	0.491	55558	0.107	33701	0.012	
Rep	<i>Atractus edioi</i>	2005	DD	DD	370	R	369	267	267	0.724	0	0.000	0	0.000	
Rep	<i>Atractus pantostictus</i>	1993	LC	LC	940260	P	714567	348087	316870	0.443	31217	0.090	19639	0.021	
Rep	<i>Atractus spinalis</i>	2013	DD	DD	763	R	480	436	433	0.902	3	0.007	249	0.326	
Rep	<i>Atractus stygius</i>	2019	-	LC	115675	P	46986	35503	31020	0.660	4483	0.126	5	0.000	
Rep	<i>Bachia bresslaui</i>	1935	VU	LC	535404	P	437936	133468	121436	0.277	12032	0.090	2949	0.006	
Rep	<i>Bachia cacerensis</i>	1998	DD	DD	365	R	364	346	333	0.915	13	0.038	0	0.000	
Rep	<i>Bachia didactyla</i>	2011	EN	EN	6466	R	6069	4931	4382	0.722	549	0.111	0	0.000	
Rep	<i>Bachia geralista</i>	2012	DD	NT	26232	R	26121	25295	22314	0.854	2981	0.118	2542	0.097	
Rep	<i>Bachia micromela</i>	2007	DD	DD	376	R	223	219	217	0.973	2	0.009	0	0.000	
Rep	<i>Bachia oxyrhina</i>	2008	LC	LC	309	R	309	308	309	1.000	-1	-0.003	309	1.000	
Rep	<i>Bachia psamophila</i>	2007	CR	CR	375	R	375	312	327	0.872	-15	-0.048	0	0.000	
Rep	<i>Bothrops itapetiningae</i>	1907	VU	NT	675437	P	413626	104262	99012	0.239	5250	0.050	3188	0.005	
Rep	<i>Bothrops marmoratus</i>	2008	LC	LC	383515	P	355425	191336	172233	0.485	19103	0.100	6706	0.018	
Rep	<i>Bothrops moojeni</i>	1866	LC	LC	2686680	W	1652810	892999	797500	0.483	95499	0.107	56071	0.021	
Rep	<i>Bothrops pauloensis</i>	1925	LC	LC	1776108	P	1077449	428354	388691	0.361	39663	0.093	16073	0.009	
Rep	<i>Chironius brazili</i>	2015	-	LC	1108760	P	499736	178334	169352	0.339	8982	0.050	8463	0.008	
Rep	<i>Coleodactylus brachystoma</i>	1935	LC	LC	477642	P	440080	255519	227210	0.516	28309	0.111	19979	0.042	
Rep	<i>Colobosaura modesta</i>	1862	LC	LC	3352590	W	1566714	943917	844865	0.539	99052	0.105	51953	0.016	
Rep	<i>Drymoluber brasili</i>	1918	LC	LC	3738607	W	1730293	968392	869782	0.503	98610	0.102	55857	0.015	
Rep	<i>Enyalius capetinga</i>	2018	-	-	2536	R	2541	1513	1467	0.577	46	0.030	439	0.173	
Rep	<i>Epicrates crassus</i>	1862	LC	LC	4378535	W	1700266	923239	830493	0.488	92746	0.100	69196	0.016	
Rep	<i>Epictia clinorostris</i>	2010	VU	LC	28685	R	28642	16650	14959	0.522	1691	0.102	110	0.004	
Rep	<i>Erythrolamprus maryellenae</i>	1985	LC	LC	1096089	P	892574	483771	436682	0.489	47089	0.097	24325	0.022	
Rep	<i>Eurolophosaurus nanuzae</i>	1981	LC	LC	21992	R	9932	7154	6674	0.672	480	0.067	483	0.022	

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Rep	<i>Gymnodactylus amarali</i>	1925	LC	LC	609460	P	528344	366236	322631	0.611	43605	0.119	28995	0.048	
Rep	<i>Gymnodactylus guttulatus</i>	1982	LC	LC	362	R	362	331	327	0.903	4	0.012	27	0.075	
Rep	<i>Helicops boitata</i>	2019	-	LC	365	R	366	326	302	0.825	24	0.074	0	0.000	
Rep	<i>Helicops gomesi</i>	1921	LC	LC	413583	P	288435	60766	60073	0.208	693	0.011	2688	0.007	
Rep	<i>Helicops phantasma</i>	2021	-	LC	88053	P	66241	55561	49465	0.747	6096	0.110	2697	0.031	
Rep	<i>Heterodactylus lundii</i>	1862	EN	VU	34452	R	34024	10410	9892	0.291	518	0.050	124	0.004	
Rep	<i>Hoplocercus spinosus</i>	1843	LC	LC	2749462	P	1304886	811809	717075	0.550	94734	0.117	58908	0.021	
Rep	<i>Kentropyx paulensis</i>	1893	LC	LC	892348	P	740947	298826	275725	0.372	23101	0.077	10957	0.012	
Rep	<i>Kentropyx vanzoi</i>	1980	NT	VU	668452	P	480400	254191	224753	0.468	29438	0.116	5750	0.009	
Rep	<i>Leposternon cerradensis</i>	2008	DD	DD	361	R	362	72	96	0.265	-24	-0.333	0	0.000	
Rep	<i>Leposternon maximus</i>	2011	LC	LC	853	R	852	767	738	0.866	29	0.038	259	0.304	
Rep	<i>Leposternon mineiro</i>	2018	-	-	726	R	726	329	278	0.383	51	0.155	0	0.000	
Rep	<i>Liophylops schubarti</i>	1948	DD	DD	709	R	709	146	144	0.203	2	0.014	0	0.000	
Rep	<i>Liophylops taylori</i>	2018	-	LC	367	R	366	309	296	0.809	13	0.042	135	0.368	
Rep	<i>Lygophis paucidens</i>	1953	LC	LC	2337650	P	1475878	904410	807705	0.547	96705	0.107	51135	0.022	
Rep	<i>Manciola guaporicola</i>	1935	LC	LC	1791497	P	929679	439087	396033	0.426	43054	0.098	27639	0.015	
Rep	<i>Micrablepharus atticolus</i>	1996	LC	LC	1165723	P	874191	418853	380022	0.435	38831	0.093	9664	0.008	
Rep	<i>Micrurus brasiliensis</i>	1967	LC	LC	626550	P	485296	385014	342342	0.705	42672	0.111	28962	0.046	
Rep	<i>Micrurus tricolor</i>	1956	LC	LC	197935	P	56582	28945	26513	0.469	2432	0.084	1083	0.006	
Rep	<i>Phalotris cerradensis</i>	2020	-	-	368	R	367	357	291	0.793	66	0.185	97	0.264	
Rep	<i>Phalotris concolor</i>	1994	DD	NT	17642	R	16006	10487	9640	0.602	847	0.081	154	0.009	
Rep	<i>Phalotris labiomaculatus</i>	2002	LC	LC	49626	R	45866	43625	39953	0.871	3672	0.084	1296	0.026	
Rep	<i>Phalotris lativittatus</i>	1994	NT	NT	122868	P	57019	9690	10216	0.179	-526	-0.054	261	0.002	
Rep	<i>Phalotris matogrossensis</i>	2005	LC	LC	841607	P	465009	140660	129725	0.279	10935	0.078	4806	0.006	
Rep	<i>Phalotris mertensi</i>	1955	LC	LC	634842	P	332409	68574	67590	0.203	984	0.014	2693	0.004	
Rep	<i>Phalotris multipunctatus</i>	1994	EN	EN	1055	P	705	103	103	0.146	0	0.000	8	0.008	
Rep	<i>Phalotris nasutus</i>	1915	LC	LC	1511881	P	960893	426438	386080	0.402	40358	0.095	8774	0.006	
Rep	<i>Philodryas livida</i>	1923	VU	VU	388737	P	233040	56365	52225	0.224	4140	0.073	1995	0.005	
Rep	<i>Philodryas mattogrossensis</i>	1898	LC	LC	724317	P	357122	95138	88960	0.249	6178	0.065	4421	0.006	
Rep	<i>Placosoma cipoense</i>	1966	EN	EN	359	R	264	237	241	0.913	-4	-0.017	224	0.624	
Rep	<i>Psilops seductus</i>	2017	-	-	737	R	737	734	572	0.776	162	0.221	314	0.426	
Rep	<i>Rhachidelus brazili</i>	1908	LC	LC	1521523	P	853610	283199	262258	0.307	20941	0.074	8198	0.005	
Rep	<i>Rhachisaurus brachylepis</i>	1974	DD	NT	28584	R	19757	13244	12568	0.636	676	0.051	2306	0.081	
Rep	<i>Salvator duseni</i>	1910	LC	LC	440647	P	405311	170287	155213	0.383	15074	0.089	11324	0.026	
Rep	<i>Siagonodon acutirostris</i>	2011	LC	LC	1494	R	1495	1392	1349	0.902	43	0.031	831	0.556	
Rep	<i>Simophis rhinostoma</i>	1837	LC	LC	1421441	P	792830	280686	263452	0.332	17234	0.061	14475	0.010	

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Groups	Species	Year	IUCN	ICMBio	T.Range	Category	C.Range	Nat2000	Nat2020	PercNat	Loss	PercLoss	ProtRange	PercProt	Capítulo 1. Hotspot getting hotter
Rep	<i>Stenocercus albolineatus</i>	2015	-	-	138504	R	71180	62072	57771	0.812	4301	0.069	96	0.001	
Rep	<i>Stenocercus canastra</i>	2019	-	LC	690	R	689	446	465	0.675	-19	-0.043	570	0.826	
Rep	<i>Stenocercus quinarius</i>	2006	LC	LC	48388	R	48381	42800	35065	0.725	7735	0.181	3601	0.074	
Rep	<i>Stenocercus sinesaccus</i>	2005	LC	LC	93473	P	93452	47443	42025	0.450	5418	0.114	110	0.001	
Rep	<i>Thamnodynastes rutilus</i>	1942	LC	LC	647749	P	541724	192840	179352	0.331	13488	0.070	6277	0.010	
Rep	<i>Trilepida brasiliensis</i>	1949	LC	LC	1503963	W	1145268	702364	628041	0.548	74323	0.106	40976	0.027	
Rep	<i>Trilepida fuliginosa</i>	2006	LC	LC	453998	P	389725	250479	225855	0.580	24624	0.098	12403	0.027	
Rep	<i>Trilepida jani</i>	2012	LC	LC	19461	R	10610	7243	6945	0.655	298	0.041	1192	0.061	
Rep	<i>Trilepida koppesi</i>	1955	LC	LC	558325	P	411406	111020	103407	0.251	7613	0.069	2470	0.004	
Rep	<i>Tropidophis precious</i>	2012	DD	NT	719	R	92	72	74	0.804	-2	-0.028	0	0.000	
Rep	<i>Tropidurus callathelys</i>	1998	LC	-	877	R	666	508	486	0.730	22	0.043	452	0.515	
Rep	<i>Tropidurus chromatops</i>	1998	LC	-	1787	R	669	512	466	0.697	46	0.090	975	0.546	
Rep	<i>Tropidurus itambere</i>	1987	LC	LC	1456252	P	1057974	428334	393699	0.372	34635	0.081	12951	0.009	
Rep	<i>Tropidurus montanus</i>	1987	LC	LC	84788	P	69719	40355	37352	0.536	3003	0.074	3047	0.036	
Rep	<i>Tropidurus oreadicus</i>	1987	LC	LC	2773708	P	1182268	778567	688003	0.582	90564	0.116	41466	0.015	
Rep	<i>Tupinambis matipu</i>	2018	-	LC	701967	P	336620	216504	190934	0.567	25570	0.118	2526	0.004	
Rep	<i>Tupinambis quadrilineatus</i>	1997	LC	LC	1572963	P	881009	591585	522409	0.593	69176	0.117	34386	0.022	
Rep	<i>Vanzosaura savanicola</i>	2014	LC	LC	112323	P	109306	91932	77420	0.708	14512	0.158	7700	0.069	
Rep	<i>Xenodon matogrossensis</i>	1993	LC	LC	213601	P	75017	36464	33513	0.447	2951	0.081	976	0.005	
Rep	<i>Xenodon nattereri</i>	1867	LC	DD	1984447	W	1392392	711120	642984	0.462	68136	0.096	40165	0.020	
Birds	<i>Alectrurus tricolor</i>	1816	VU	VU	2797153	P	1165253	480721	437702	0.376	43019	0.089	31263	0.011	
Birds	<i>Alipiopsitta xanthops</i>	1824	NT	LC	2950314	W	1688086	981708	877060	0.520	104648	0.107	69436	0.024	
Birds	<i>Antilophia galeata</i>	1823	LC	LC	2692714	W	1720875	958996	858751	0.499	100245	0.105	58635	0.022	
Birds	<i>Arremon flavirostris</i>	1838	LC	LC	1473172	P	986460	376534	346476	0.351	30058	0.080	15613	0.011	
Birds	<i>Asthenes luizae</i>	1990	NT	EN	24900	R	16397	13487	12703	0.775	784	0.058	1989	0.080	
Birds	<i>Augastes scutatus</i>	1824	LC	LC	53428	R	33304	21296	20239	0.608	1057	0.050	3537	0.066	
Birds	<i>Celeus obrieni</i>	1973	VU	VU	825273	R	629653	478330	422126	0.670	56204	0.118	31799	0.039	
Birds	<i>Cercomacra ferdinandi</i>	1928	NT	NT	269082	P	111835	93759	83782	0.749	9977	0.106	9616	0.036	
Birds	<i>Charitospiza eucoema</i>	1905	NT	LC	3270074	W	1835450	1067750	959545	0.523	108205	0.101	59197	0.018	
Birds	<i>Cinclodes espinhaensis</i>	2012	-	EN	2941	R	2141	1441	1442	0.674	-1	-0.001	454	0.154	
Birds	<i>Clibanornis rectirostris</i>	1831	LC	LC	1678654	P	1062485	434936	399466	0.376	35470	0.082	20477	0.012	
Birds	<i>Columbina cyanopis</i>	1870	CR	CR	2172	P	1561	897	833	0.534	64	0.071	264	0.122	
Birds	<i>Conothraupis mesoleuca</i>	1939	EN	EN	144734	P	124839	69491	62536	0.501	6955	0.100	1853	0.013	
Birds	<i>Coryphaspiza melanotis</i>	1822	VU	VU	3576856	P	1654928	944067	852145	0.515	91922	0.097	55246	0.015	
Birds	<i>Cyanocorax cristatellus</i>	1823	LC	LC	4033939	W	1889315	1091882	982901	0.520	108981	0.100	69579	0.017	
Birds	<i>Embernagra longicauda</i>	1844	LC	LC	218284	P	55348	35864	34351	0.621	1513	0.042	3818	0.018	

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Groups	Species	Year	IUCN	ICMBio	T.Range	Category	C.Range	Nat2000	Nat2020	PercNat	Loss	PercLoss	ProtRange	PercProt	Capítulo 1. Hotspot getting hotter
Birds	<i>Euscarthmus rufomarginatus</i>	1868	NT	LC	3904841	W	1601267	962972	858020	0.536	104952	0.109	60224	0.015	
Birds	<i>Geositta poeciloptera</i>	1830	VU	VU	1987612	P	1313523	600880	545566	0.415	55314	0.092	25237	0.013	
Birds	<i>Guyramemua affine</i>	1856	NT	LC	2385983	P	1418713	846691	754012	0.532	92679	0.109	57811	0.024	
Birds	<i>Herpsilochmus longirostris</i>	1868	LC	LC	2359869	P	1509081	807127	727067	0.482	80060	0.099	46636	0.020	
Birds	<i>Hydropsalis candidans</i>	1867	VU	EN	1108625	P	441045	127648	118294	0.268	9354	0.073	6128	0.006	
Birds	<i>Knipolegus franciscanus</i>	1928	LC	VU	250655	P	214774	142756	125976	0.587	16780	0.118	7248	0.029	
Birds	<i>Laterallus xenopterus</i>	1934	VU	EN	835712	P	725437	287436	262674	0.362	24762	0.086	14436	0.017	
Birds	<i>Melanopareia torquata</i>	1831	LC	LC	3451937	W	1796343	1017597	913971	0.509	103626	0.102	58797	0.017	
Birds	<i>Microspingus cinereus</i>	1850	LC	LC	1081620	P	806571	331291	305178	0.378	26113	0.079	13734	0.013	
Birds	<i>Myiothlypis leucophrys</i>	1868	LC	LC	1694948	P	1293285	636994	572190	0.442	64804	0.102	27987	0.017	
Birds	<i>Neothraupis fasciata</i>	1823	NT	LC	4017704	W	1822371	1039613	932760	0.512	106853	0.103	72913	0.018	
Birds	<i>Nothura minor</i>	1825	VU	EN	1222422	P	848348	281814	261373	0.308	20441	0.073	6810	0.006	
Birds	<i>Nyctiprogne viellardi</i>	1994	LC	EN	47687	R	34488	23606	22173	0.643	1433	0.061	864	0.018	
Birds	<i>Nystalus striatipectus</i>	1854	-	LC	263013	P	154180	48573	43668	0.283	4905	0.101	1112	0.004	
Birds	<i>Paroaria baeri</i>	1907	LC	LC	83135	P	80744	64101	59668	0.739	4433	0.069	9157	0.110	
Birds	<i>Penelope ochrogaster</i>	1870	VU	NT	1054646	P	833483	486470	437183	0.525	49287	0.101	24593	0.023	
Birds	<i>Phaethornis nattereri</i>	1887	LC	LC	2109777	P	866893	646737	571652	0.659	75085	0.116	42917	0.020	
Birds	<i>Phyllomyias reiseri</i>	1905	LC	EN	750210	P	677504	331300	295224	0.436	36076	0.109	17866	0.024	
Birds	<i>Phylloscartes roquettei</i>	1928	EN	EN	240589	P	179541	114474	106492	0.593	7982	0.070	7195	0.030	
Birds	<i>Polystictus superciliaris</i>	1831	LC	LC	442086	P	166888	79076	75493	0.452	3583	0.045	6555	0.015	
Birds	<i>Porphyrospiza caerulescens</i>	1830	NT	LC	3175252	W	1633187	1001974	899222	0.551	102752	0.103	74553	0.024	
Birds	<i>Pyrrhura pfrimeri</i>	1920	EN	EN	13772	R	13786	8738	7463	0.541	1275	0.146	557	0.040	
Birds	<i>Saltatricula atricollis</i>	1817	LC	LC	4504410	W	1888061	1093686	984020	0.521	109666	0.100	77308	0.017	
Birds	<i>Scytalopus novacapitalis</i>	1958	EN	EN	89692	P	88938	32515	30320	0.341	2195	0.068	1284	0.014	
Birds	<i>Sporophila nigrorufa</i>	1837	VU	VU	107707	P	10043	5558	4627	0.461	931	0.168	11182	0.104	
Birds	<i>Synallaxis simoni</i>	1907	LC	LC	61720	P	59631	46840	43393	0.728	3447	0.074	8243	0.134	
Birds	<i>Syndactyla dimidiata</i>	1859	LC	LC	1196783	P	868531	347561	318901	0.367	28660	0.082	15177	0.013	
Birds	<i>Taoniscus nanus</i>	1815	EN	EN	1308726	P	849901	325050	297658	0.350	27392	0.084	15832	0.012	
Birds	<i>Uropelia campestris</i>	1825	LC	LC	4642794	W	1669036	1009121	902911	0.541	106210	0.105	71821	0.016	
Mam	<i>Akodon kadiweu</i>	2021	-	DD	356	R	357	322	324	0.908	-2	-0.006	93	0.261	
Mam	<i>Akodon lindberghi</i>	1990	DD	LC	2844	P	899	570	574	0.639	-4	-0.007	569	0.200	
Mam	<i>Calassomys apicalis</i>	2014	-	NT	584	R	584	575	575	0.985	0	0.000	412	0.706	
Mam	<i>Callithrix penicillata</i>	1812	LC	LC	1301874	P	806133	420573	380919	0.473	39654	0.094	21794	0.017	
Mam	<i>Calomys tocantinsi</i>	2003	LC	LC	155446	P	69838	61853	58034	0.831	3819	0.062	9269	0.060	
Mam	<i>Carterodon sulcidens</i>	1838	DD	DD	1099681	P	897277	394486	354934	0.396	39552	0.100	5637	0.005	
Mam	<i>Cerradomys akroai</i>	2014	-	DD	748	R	749	722	693	0.925	29	0.040	275	0.368	

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Groups	Species	Year	IUCN	ICMBio	T.Range	Category	C.Range	Nat2000	Nat2020	PercNat	Loss	PercLoss	ProtRange	PercProt	Capítulo 1. Hotspot getting hotter
Mam	<i>Cerradomys marinhus</i>	2003	LC	LC	291448	P	265162	133048	118434	0.447	14614	0.110	7898	0.027	
Mam	<i>Cerradomys scotti</i>	2002	LC	LC	2281453	W	1435144	722350	649403	0.453	72947	0.101	46800	0.021	
Mam	<i>Clyomys laticeps</i>	1909	LC	LC	1373496	P	988242	370852	340536	0.345	30316	0.082	13027	0.010	
Mam	<i>Ctenomys bicolor</i>	1914	-	EN	108826	P	83906	57887	49839	0.594	8048	0.139	5	0.000	
Mam	<i>Ctenomys nattereri</i>	1848	LC	LC	195476	P	52650	37284	33118	0.629	4166	0.112	15090	0.077	
Mam	<i>Euryoryzomys lamia</i>	1901	VU	EN	45977	R	45632	22486	20836	0.457	1650	0.073	731	0.016	
Mam	<i>Galea flavidens</i>	1835	LC	-	1324021	P	1095629	704416	625150	0.571	79266	0.113	38848	0.029	
Mam	<i>Gyldenstolpia planaltensis</i>	1972	-	EN	1104	R	934	504	456	0.488	48	0.095	167	0.151	
Mam	<i>Holochilus sciureus</i>	1842	LC	LC	668490	P	579570	408680	358233	0.618	50447	0.123	32800	0.049	
Mam	<i>Hylaeamys acritus</i>	2005	DD	-	63007	P		NA	NA	NA	NA	NA	6940	0.110	
Mam	<i>Juscelinomys candango</i>	1965	EX	CR	366	R	365	162	146	0.400	16	0.099	83	0.227	
Mam	<i>Juscelinomys huanchacae</i>	1999	DD	-	1201	R		NA	NA	NA	NA	NA	1201	1.000	
Mam	<i>Kerodon acrobata</i>	1997	DD	VU	6089	R	6091	4202	3513	0.577	689	0.164	0	0.000	
Mam	<i>Kunsia tomentosus</i>	1830	LC	LC	3560689	P	1084730	450627	408600	0.377	42027	0.093	30019	0.008	
Mam	<i>Lonchophylla bokermanni</i>	1978	EN	VU	33611	R	12323	10385	9878	0.802	507	0.049	1197	0.036	
Mam	<i>Lonchophylla dekeyseri</i>	1983	EN	EN	1888936	P	1233382	843453	752400	0.610	91053	0.108	54623	0.029	
Mam	<i>Lycalopex vetulus</i>	1842	NT	VU	2865103	W	1751355	1018134	916241	0.523	101893	0.100	55754	0.020	
Mam	<i>Microakodontomys transitorius</i>	1993	EN	EN	733	R	733	517	508	0.693	9	0.017	318	0.434	
Mam	<i>Monodelphis kunsi</i>	1975	LC	LC	3347924	P	1395007	668384	604014	0.433	64370	0.096	43365	0.013	
Mam	<i>Monodelphis sanctaerosae</i>	2012	-	-	734	R	369	305	290	0.786	15	0.049	0	0.000	
Mam	<i>Oecomys cleberi</i>	1981	DD	LC	833008	P	627621	221133	201750	0.322	19383	0.088	4694	0.006	
Mam	<i>Oligoryzomys moojeni</i>	2005	DD	LC	297359	P	277383	200570	175394	0.632	25176	0.126	21823	0.073	
Mam	<i>Oligoryzomys rupestris</i>	2005	DD	EN	1470	P	480	472	472	0.983	0	0.000	401	0.273	
Mam	<i>Oxymycterus delator</i>	1903	LC	LC	2415453	W	1489969	787419	715046	0.480	72373	0.092	48077	0.020	
Mam	<i>Oxymycterus itapeby</i>	2019	-	DD	1045	R	598	168	178	0.298	-10	-0.060	0	0.000	
Mam	<i>Phyllomys brasiliensis</i>	1840	EN	EN	2411	R	2410	879	903	0.375	-24	-0.027	107	0.044	
Mam	<i>Phyllomys centralis</i>	2018	-	-	1334	R	1333	633	592	0.444	41	0.065	57	0.043	
Mam	<i>Rhipidomys ipukensis</i>	2011	DD	LC	34446	R	17078	14692	13080	0.766	1612	0.110	4699	0.136	
Mam	<i>Rhipidomys macrurus</i>	1855	LC	LC	1976730	W	1342010	664719	604971	0.451	59748	0.090	40196	0.020	
Mam	<i>Thalpomys cerradensis</i>	1990	LC	VU	957821	P	724331	508190	448195	0.619	59995	0.118	33989	0.036	
Mam	<i>Thalpomys lasiotis</i>	1916	LC	EN	194904	P	181837	79032	73348	0.403	5684	0.072	4384	0.023	
Mam	<i>Thrichomys apereoides</i>	1839	LC	LC	362360	P	258704	153984	142781	0.552	11203	0.073	10204	0.028	
Mam	<i>Thrichomys pachyurus</i>	1845	LC	LC	762797	P	568344	337552	302660	0.533	34892	0.103	13812	0.018	
Mam	<i>Thylamys velutinus</i>	1842	NT	LC	472911	P	377019	115290	109906	0.292	5384	0.047	3827	0.008	
Mam	<i>Trinomys moojeni</i>	1992	EN	EN	1403	R	1031	769	765	0.742	4	0.005	332	0.237	

567 Appendix S2 - Figures

568 Figure S1

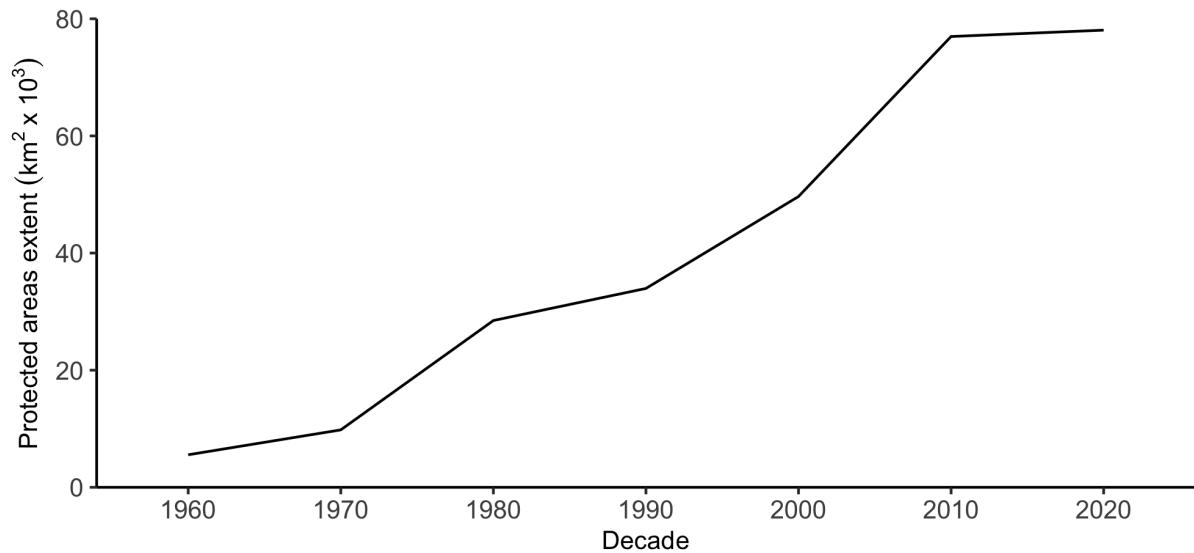


Figure S1 - Cerrado's Strict Protection Protected Areas (PAs) area accumulation throughout time (according to [UNEP-WCMC & IUCN, 2023](#)).

569 Figure S2

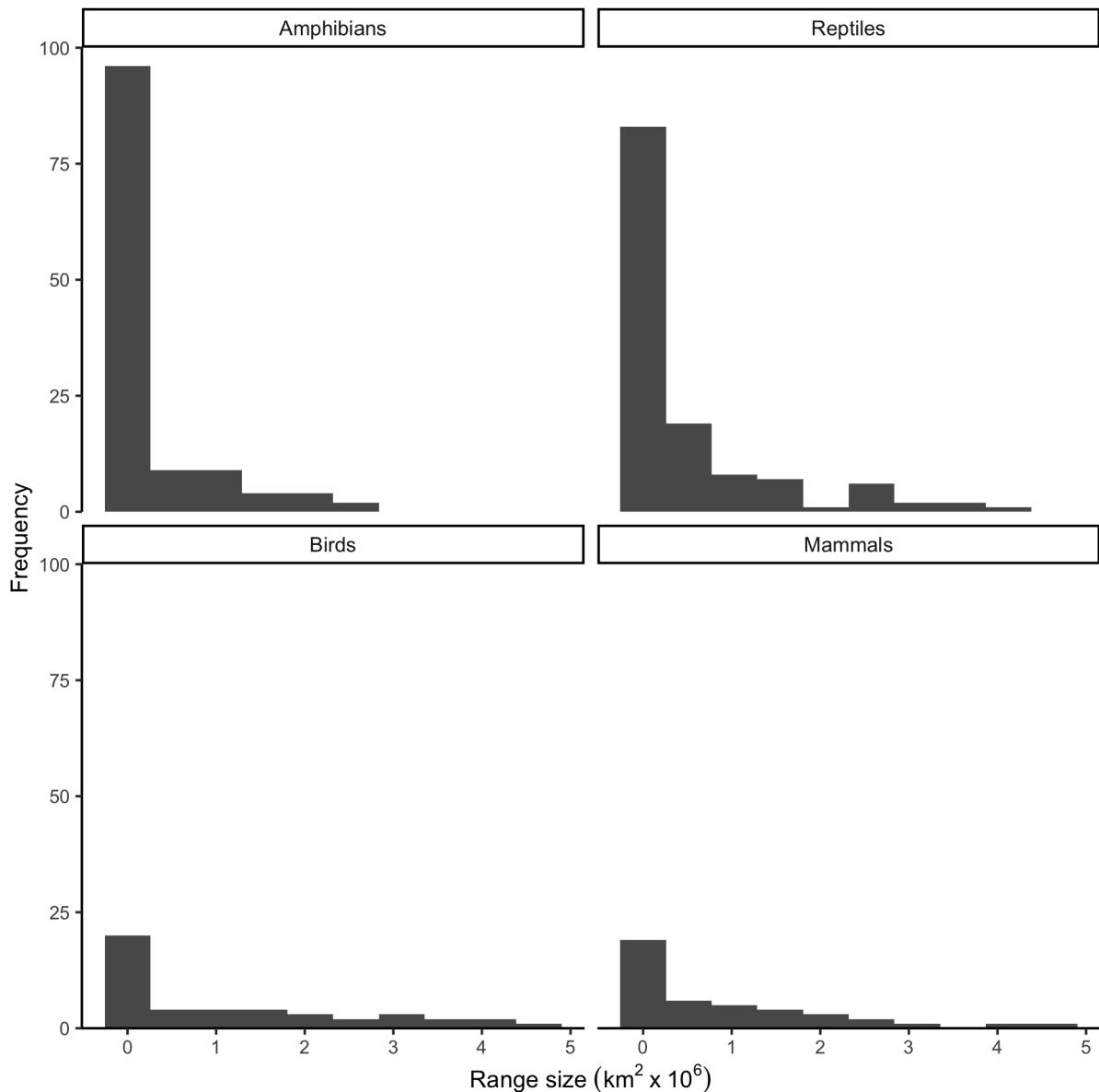


Figure S2 - Histograms of range size frequencies in each terrestrial vertebrate group

570 Figure S3

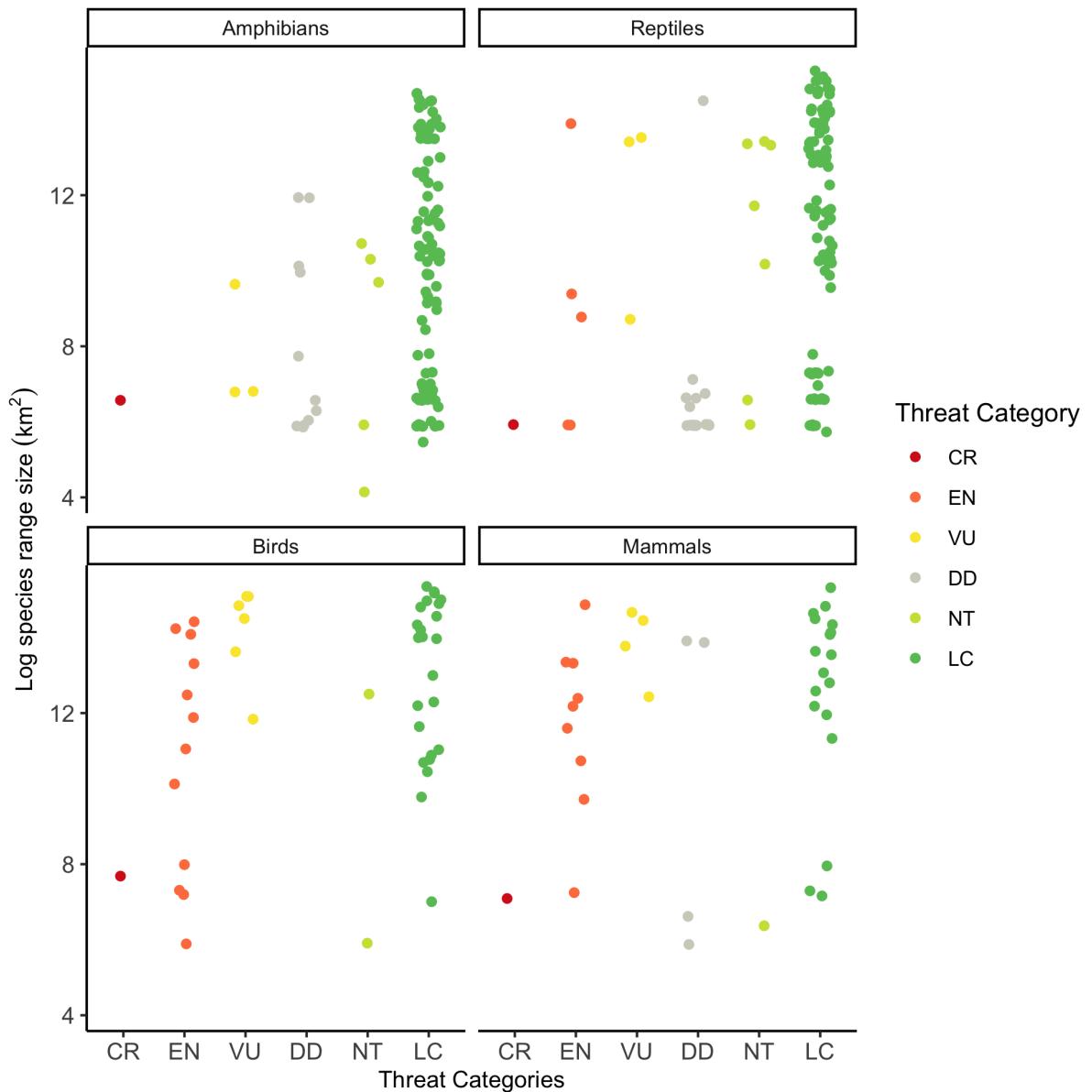


Figure S3 - Range size variation in each terrestrial vertebrate group according to ICMBio's threat categories

571 Figure S4

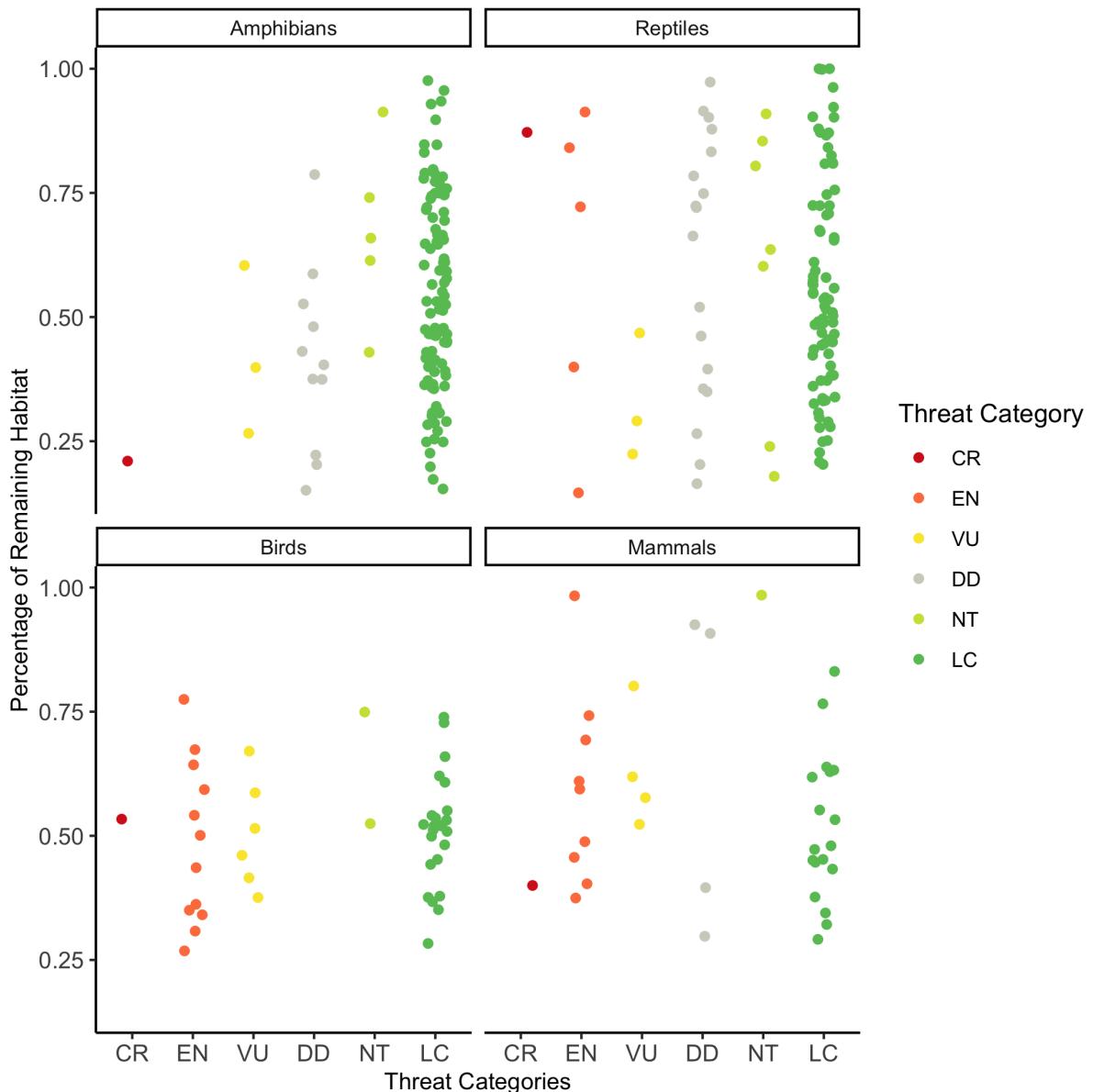


Figure S4 - Percentual habitat loss variation in each terrestrial vertebrate group according to ICMBio's threat categories

572 Figure S5

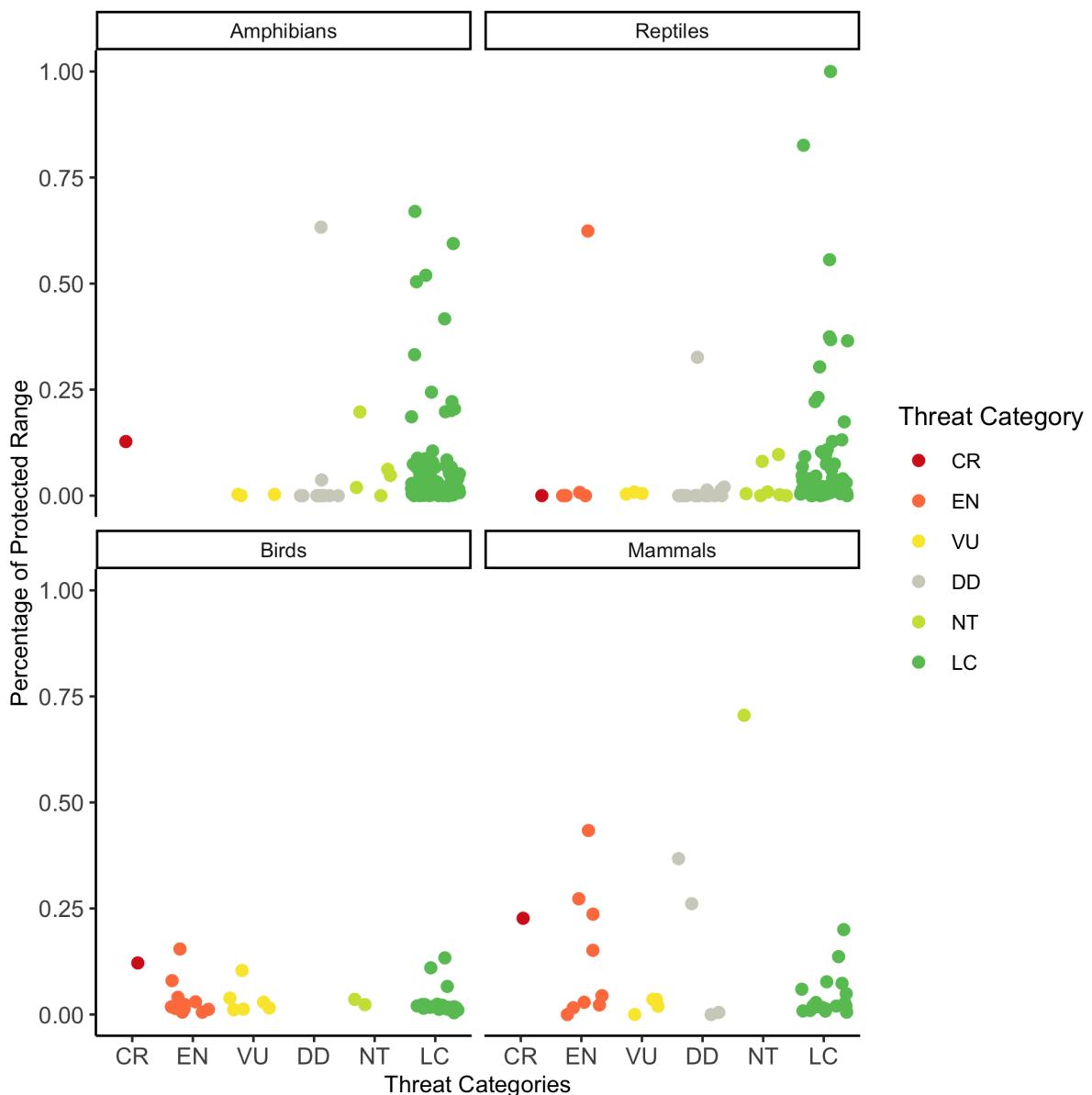


Figure S5 - Percentual protected range variation in each terrestrial vertebrate group according to ICMBio's threat categories

573 2 In search of generality: revised distribution data and regionalization of Cerrado endemic tetrapods

574

Abstract

575 **Aim:** To search for a general regionalization pattern using verified records of endemic
576 terrestrial vertebrates. To test previous hypotheses of congruent distribution patterns for
577 Cerrado biotas. To study the role of elevation as a driver of endemism and distribution
578 in the Cerrado region.

579 **Location:** Cerrado domain, central South America

580 **Taxon:** Tetrapoda

581 **Methods:** We used a species occurrence matrix to implement a Biotic Element analy-
582 sis to test for non-random spatial congruence of raw distributions of Cerrado endemic
583 amphibians, reptiles, birds, and mammals. We implemented multiple linear regression
584 on elevational records of species comparing the average elevational range of all delimited
585 Biotic Elements (BE).

586 **Results:** We compiled and revised 13,800 unique distribution records of 340 Cerrado en-
587 demic tetrapods and detected a significant, non-random co-distribution pattern formed by
588 29 Biotic Elements comprising 182 species, and corroborating the first general prediction
589 of the vicariant model. Most BEs were composed of at least three vertebrate groups, re-
590 flecting general tetrapod endemism patterns. Congeneric species were segregated among
591 different BEs corroborating the second major prediction of the vicariant model. Our
592 regionalization scheme was broadly congruent with previous results, and revealed three
593 previously undetected areas. Most (89%) partial or restricted BEs are clearly segregated
594 in elevation, and we recognized 14 “Plateau units” and 12 “Depression units”.

595 **Main conclusions:** Our results support an emergent consensual biotic regionalization
596 pattern in the Cerrado. We also revealed three novel regions and complex biogeographical
597 patterns. The clear altitudinal segregation among Biotic Elements corroborates previous
598 ideas on the role of geomorphological changes in shaping Cerrado and Neotropical ende-
599 mism patterns. Our recovered units should serve as a template for the description of new
600 taxa, for delimiting poorly studied ranges, and for guiding urgent conservation action in
601 the Cerrado.

602

603 **Keywords:** Biodiversity, Bioregions, Biotic Elements, Elevation, Endemism, Tetrapods,
604 Vicariance

605 2.1 Introduction

606 Understanding general patterns of biotic distribution is a long-standing scientific
607 challenge (e.g. J. H. Brown, 1995), and provide central empirical and theoretical elements
608 to Evolutionary Biology, Biogeography and Biological Conservation (Holt et al., 2013;
609 Kreft & Jetz, 2010; Whittaker, Riddle, Hawkins, & Ladle, 2013). The argument on how
610 different areas are occupied by co-distributed biotas dates back to the eighteenth century,
611 with the proposition of the “Buffon’s Law” by the French naturalist Georges-Louis Leclerc
612 (“Earl of Buffon”, see C. B. Cox et al., 2016). Key advances in the following century by
613 Sclater (1858) and Wallace (1876), proposing the first (and still largely undisputed - see
614 Holt et al., 2013) global map of zoogeographical realms, based on raw distribution data
615 for birds and mammals, laid the foundation for the science known today as Biogeography
616 (C. B. Cox et al., 2016). The validation of previous results allowed the understanding of
617 large-scale regionalization patterns and their drivers (see Ficetola et al., 2017).

618 Despite these enduring results on global Zoogeographical realms (Holt et al., 2013;
619 Sclater, 1858; Wallace, 1876), studies of biogeographical patterns at more refined, conti-
620 nental scales are proportionally scarcer, with few studies aiming to test coincident distri-
621 bution patterns based on data from different groups of organisms, and using quantitative,
622 objective methods (see Edler, Guedes, Zizka, Rosvall, & Antonelli, 2017; Holt et al.,
623 2013). This limitation results mainly from the paucity of good quality, detailed, point
624 locality data for most organisms and in most continents (Holt et al., 2013), and is known
625 as the Wallacean shortfall (Whittaker et al., 2005). As a result, biogeographical studies
626 generally include data only from particular clades or groups of organisms, and general
627 patterns based on larger taxonomic units are rarely documented and tested at continen-
628 tal or subcontinental scales (Holt et al., 2013; Kreft & Jetz, 2010). As a consequence,
629 regional biotic subdivisions and resulting spatial units in biogeography are often defined
630 arbitrarily (Edler et al., 2017; Kreft & Jetz, 2010).

631 If high-quality, reliable species distribution data is available, the difficulties related to
632 delimiting biogeographical units should decrease when large and diverse groups of taxa are
633 analysed (Kreft & Jetz, 2010; Nelson & Platnick, 1981). Indeed, geological processes that
634 modify large areas should affect the geographical distribution of entire biotas, formed by
635 different groups of organisms (Wiley, 1988), so that these groups will tend to share similar
636 patterns of distribution and endemism (Hausdorf, 2002; Wiley, 1988). In the megadiverse
637 Neotropics, however, large gaps in basic faunistic knowledge have hampered broader,
638 comprehensive, multi-taxon analyses of endemism and biotic regionalization (Holt et al.,
639 2013; Kreft & Jetz, 2010). This lack of studies is also verified in the savannas that

Essa é a segunda versão desse artigo, submetido com *major revisions* ao *Journal of Biogeography*. Em 05 de junho de 2023 recebemos uma segunda revisão, atualmente (18 de julho) em preparo para resubmissão. Esse texto foi produzido com a colaboração de: Ana Paula Carmignotto, Ricardo Jannini Sawaya, Luis Fabio Silveira, Paula Hanna Valdujo e Cristiano de Campos Nogueira

640 dominate the central portion of South America, in the biodiversity hotspot known as
641 Cerrado, the richest and most imperilled tropical savanna in the globe (Colli et al., 2020).

642 Until recently, analyses on Cerrado endemism and biotic regionalization were scarce
643 and based on limited data (Colli et al., 2020). Earlier studies described Cerrado vertebrate
644 biotas as impoverished, poor in endemics and dominated by widespread, generalist taxa
645 (see Sick, 1965; Vanzolini, 1963). The first zoogeographical interpretations of the Cerrado
646 (Vanzolini, 1963), based on the distribution of reptiles, proposed two major areas of en-
647 demism, a septentrional (Northeastern) and a meridional (Southwestern) portion. Later,
648 Silva (1997), recovered four areas of endemism, based on the distributions of endemic
649 bird species, all coincident with major topographic units in central Brazil (Silva, 1997).
650 Despite centuries of scarcity of data, targeted inventories in the last three decades and
651 recent analyses led to important advances in the understanding of the Cerrado terres-
652 trial vertebrate fauna (Azevedo et al., 2016; Carmignotto et al., 2012; Nogueira et al.,
653 2010; Valdujo et al., 2012). These new inventories led to the discovery and description
654 of hundreds of new vertebrate species, many endemic to central Brazil (see examples in
655 Nogueira et al., 2010) and often showing localized ranges (see trends in Gaston, 1996).
656 However, drivers of distribution and endemism patterns in central Brazil are still poorly
657 understood, and the importance of landscape evolution, climatic stability, and vicariance
658 have just started to be acknowledged (Azevedo et al., 2016; Carmignotto et al., 2022;
659 Lopes, 2008; Nogueira et al., 2011; Silva, 1997; Werneck, 2011). In this scenario of ra-
660 pid data accumulation and rampant habitat loss (see Colli et al., 2020), understanding
661 endemism patterns at refined scales becomes even more urgent (see Brooks et al., 2006),
662 especially when neither biodiversity nor threats are equally distributed throughout the
663 territory (e.g. Azevedo et al., 2016; Francoso et al., 2020; Strassburg et al., 2017).

664 Recent analyses on the more extensive distributional database of endemic squamate
665 reptiles and anurans (Azevedo et al., 2016; Nogueira et al., 2011), provided the first quan-
666 titative analyses of regionalization patterns of the Cerrado endemic fauna. The complex
667 and novel endemism patterns revealed in these studies were largely defined by topographi-
668 cal divisions between large, ancient flatland plateaus and younger peripheral depressions,
669 corroborating earlier biogeographical interpretations (K. S. Brown & Gifford, 2002; Silva
670 & Bates, 2002). Additionally, elevation has been recovered as a major driver of assemblage
671 dissimilarity in Cerrado amphibians (Valdujo, Carnaval, & Graham, 2013) and therefore
672 is likely to be related to the formation of regionalized species groups. The insular con-
673 dition of Cerrado plateaus is also pointed as a potential determinant of endemism in the
674 plant genus Mimosa, that peaks in upland interfluvial savannas and grasslands of central
675 Brazil (Simon & Proença, 2000). However, all these studies involved limited groups of
676 organisms, and their conclusions may not reflect general patterns for entire biotas. Com-
677 bining distributional data of all tetrapod groups should enhance the chance of detecting
678 a general, significant biogeographical signal, resulting from large-scale historical processes

679 that affected different groups of organisms, despite their broad ecological differences (Roll
680 et al., 2017).

681 We aimed herein to (1) test previous hypotheses of congruent distributional patterns
682 in the Cerrado based on the first revised and updated distributional dataset including all
683 known Cerrado endemic tetrapods; (2) test the role of elevation (plateaus x depressions) as
684 a potential driver of Cerrado terrestrial vertebrate endemism; and (3) propose a robust,
685 objective and general biogeographical regionalization scheme for the richest and most
686 endangered tropical savanna on the planet, supported by a large, revised point-locality
687 database for tetrapods, one of the best studied groups of organisms (see Gaston, 1996;
688 Roll et al., 2017).

689 2.2 Materials and Methods

690 2.2.1 Study area

691 The Cerrado is the largest savanna in the Neotropics, and occupies a central position
692 in South America, along ancient uplands of the Brazilian shield, separating lowland open
693 areas of the Caatinga in the northeast from the Chaco in the southwest, and also dividing
694 Amazonian in the northwest from the Atlantic Forest in the southeast. The Cerrado vege-
695 tation is dominated by upland savannas and grasslands, along extensive ancient plateaus,
696 intermingled by peripheral, mostly forested depressions, associated with upper portions of
697 major drainages of South America (Tocantins-Araguaia, Paraná, Paraguay, Guaporé, and
698 São Francisco, Ab'Sáber (1998)). These topographical and edaphic conditions generate a
699 complex landscape mosaic of grassland and savanna, crossed by palm marshes and gallery
700 forests along drainages (Eiten, 1972; Ratter et al., 1997), a pattern observed both at local
701 and continental scales, forming complex, horizontally stratified landscapes (Colli et al.,
702 2020; Silva & Bates, 2002).

703 Despite being considered a global biodiversity hotspot (Myers et al., 2000) the re-
704 gion is still poorly protected and remains under strong pressure from the expansion of
705 agricultural activities (Grande, Aguiar, & Machado, 2020; P. Pacheco et al., 2021; Stras-
706 sburg et al., 2017). Of the approximately 200 million hectares covered by Cerrado, only
707 19.8% remain intact and only 7.5% are legally protected. Meanwhile, recent (2002-2011)
708 rates of deforestation were 2.5 times higher than in Amazonia (Strassburg et al., 2017).

709 2.2.2 Data sources

710 Our database was built based on three major sources: 1 - standardized field surveys
711 planned to fill previous sampling gaps in the Cerrado (see Carmignotto et al., 2022;
712 Nogueira et al., 2009; Valdujo et al., 2012), 2 - broad revision of vouchered specimens
713 deposited in major scientific collections, and 3 - compilation of reliable records in the

714 taxonomic literature (details in Carmignotto et al., 2022; Nogueira et al., 2019, 2009;
715 Valdujo et al., 2012). We did not include records from online digitized biodiversity data
716 (such as GBIF or similar electronic databases, that often comprise error-prone, raw data,
717 see Nogueira et al., 2019, and references therein).

718 We updated the list of Cerrado endemic terrestrial vertebrate species presented in
719 previous studies (Azevedo et al., 2016; Carmignotto et al., 2012; Gutiérrez & Marinho-
720 Filho, 2017; Nogueira et al., 2011; Silva, 1997), and used only verified point-locality records
721 to map geographical ranges of Cerrado endemic terrestrial vertebrate species (listed in
722 Appendix S1 in Supporting information). We considered as endemic those species whose
723 ranges are fully or largely coincident with the approximate limits of the Cerrado provided
724 in Dinerstein et al. (2017, see also IBGE, 1993; Olson et al., 2001). Species with marginal
725 records in transitional areas between the Cerrado and other domains, but with local
726 ranges associated with typical Cerrado habitats, were also considered endemic, due to
727 their possible historical association to once continuous savannas (currently isolated as
728 disjunct areas).

729 The taxonomy follows specific literature for each vertebrate group (Frost, 2020 for
730 amphibians, Uetz et al., 2020 for lizards/amphisbaenians, Nogueira et al., 2019 for snakes,
731 J. F. Pacheco et al., 2021 for birds, and Abreu et al., 2021 for mammals). We included
732 in our analyses species described up to early January 2021.

733 2.2.3 Analyses

734 We obtained a presence-absence matrix via the intersection of revised point-locality
735 records and 244 1° x 1° grid cells covering the Cerrado (Dinerstein et al., 2017). We
736 used the same grid size and position (grid origin) as in Azevedo et al. (2016), to make
737 results more comparable. Subsequently, we created a dissimilarity matrix based on the
738 presence-absence matrix using the geco coefficient. As in Azevedo et al. (2016), we found
739 our 1° x 1° grid relatively coarse compared to our point-locality dataset and therefore we
740 set the required geco tuning constant to $f = 0.2$ (see Hennig & Hausdorf, 2006 for a more
741 detailed explanation about the geco coefficient).

742 We then used this matrix to implement a Biotic Element analysis in ‘prabclus’
743 (Hausdorf & Hennig, 2003; Hennig & Hausdorf, 2020), an add-on package for the statisti-
744 cal software R (available at <http://cran.r-project.org>). This analysis provides a test
745 for the first major prediction of the vicariance model: non-random congruence of species
746 ranges as a result of allopatric speciation, caused by the emergence of biogeographical bar-
747 riers (Hausdorf & Hennig, 2006). Therefore, we should be able to detect groups of species
748 whose ranges are more similar to each other than to ranges of species assigned to other
749 such groups, even in the presence of limited dispersal and peripheral sympatry (Hausdorf,
750 2002; Hausdorf & Hennig, 2003). To do so, we compared the geographical ranges using the
751 function ‘prabtest’ which is a parametric bootstrap test for the non-random congruence

of species distributions. Null models were generated producing artificial ranges based on parameters (richness per cell, range size distributions, and patterns of spatial correlation and disjunction) obtained from the original dataset (Hennig & Hausdorf, 2004). The test statistic T derives from the assumption that if clusters of ranges are present in the dataset, geographical distances among clustered ranges should be smaller than distances between ranges simulated at random. This statistic is calculated as the ratio between the 25% smallest and the 25% largest distances, and it is expected to be smaller than expected by chance if ranges are clustered, and larger for homogeneous, non-regionalized data (Hennig & Hausdorf, 2004). Then, the distribution of the statistical test under null models was approximated by Monte Carlo simulation (1,000 replicates).

According to the second major prediction of the vicariance model, closely related species should be distributed among different biogeographical units, as an effect of biogeographical barriers and the fragmentation of ancestral ranges followed by speciation (Hausdorf & Hennig, 2003, 2006; Wiley, 1988). To verify if species of the same genus were segregated among different Biotic Elements (hereafter “BEs”), we implemented a chi-square test in ‘prabclus’ (function ‘*comp.test*’; Hennig & Hausdorf, 2020). If a non-significant result is found, i. e. closely related species are not clustered in the same BEs, then the second major prediction of vicariance is corroborated, with evidence of lineage fragmentation across different areas.

In addition to the test of vicariant predictions via Biotic Element analysis, we examined if species predominantly occurring in plateaus or depressions were scattered among different BEs or clustered in the same units. To do so, we also implemented a chi-square test in ‘prabclus’ (function ‘*comp.test*’; Hennig & Hausdorf, 2020). A significant result, i.e. BEs formed predominantly by species from the same altitudinal compartment (plateau/depression), indicates elevation as a putative driver of isolation among endemic Cerrado biotas. To classify species as typical of plateaus or depressions we compared elevation records to a random sample of 1000 records in the Cerrado, using a Kruskal-Wallis test (see Nogueira et al., 2011, for similar analyses). Species with significant results and showing median elevation value above or below 500 m (see Silva, 1997) were classified as plateau or depression species, respectively. Species with non-significant results but with 75% of records (defined by the limit of the 1st or 3rd quartile) above or below the 500 m were classified as plateau or depression species, respectively. The remaining species were classified as showing a general altitudinal range. Similarly, BEs were also classified as plateau, depression or general according to these same criteria.

2.2.4 Mapping

We clustered species ranges using the hierarchical method (function ‘*hprabclust*’) in ‘prabclus’. This method clusters distributions by taking the h-cut partition of hierarchical clustering and declaring all members of too small clusters as noise. This gives a

790 distance-based clustering method, which estimates the number of clusters and allows for
791 noise/non-clustered ranges (Hennig & Hausdorf, 2020). The function ‘*hprabclust*’ requires
792 two main parameters: a) the *cutdist* - a value of the h-cut partition, and b) the *nnout* -
793 the minimum number of species demanded to recognize a cluster. Smaller *nnout* values
794 allow the detection of higher numbers of BEs by recognizing clusters with at least two
795 species (when *nnout* = 1, i. e. the smallest possible composition of an area of endemism,
796 Hausdorf, 2002) while assigning fewer species to the noise component. However, as the
797 number of species in a dataset increases, we should expect an increased number of species
798 in the noise component (from the formula $k = \text{number of species}/40$, used in Hausdorf &
799 Hennig, 2003, where k is a constant that represents an initial estimate of noise, see Byers
800 & Raftery, 1998, for detailed explanations). Therefore, to reduce as much subjectivity as
801 possible in the choice of these clustering parameters, we compared combinations of *cutdist*
802 between 0.10 and 0.50 (dissimilarity values within clusters) by increases of 0.05, and *nnout*
803 between one and five (two to six species to recognize a cluster), and only pre-visualized
804 cluster outcomes where the proportion of ‘Noise/Number of BEs’ was near the estimated
805 k value (8.5 in the present study; see Appendix S2 in Supporting information). We regard
806 this as a conservative approach in the detection of BEs by hierarchical clustering.

807 To optimize parameter comparisons, we used the function ‘*cdn*’ from the package
808 ‘mapar’ (Vieira-Alencar, 2022). To check the spatial contiguity of units for each relevant
809 *cutdist-nnout* combination, we pre-visualized the resulting BEs, as well as their component
810 species and percentage of species per grid cell, using the ‘*mapar*’ function, also from
811 the ‘mapar’ package, in R environment. Finally, to illustrate detected units we chose
812 a combination of *cutdist* and *nnout* that maximized dissimilarity between BEs while
813 preserving spatial contiguity within units.

814 Following Nogueira et al. (2019), we classified species ranges as “restricted”, “partial”
815 or “widespread” based on their extent in relation to the study region (see Appendix S1).
816 Restricted range species are those with known records concentrated in a relatively small
817 geographical area (typically smaller than 50,000 km², see Eken et al., 2004); partially
818 distributed species are those recorded only at a given portion of the study region (typically
819 up to half of the entire region); and widespread species are those recorded in most or all
820 of the study region. Then, for the purpose of description, we classified BEs according to
821 the most common category of ranges among their component species.

822 We mapped the detected Biotic Elements selecting the group of grid cells that
823 contained at least one record of its component species. Grid cells with more than 70%
824 of component species were considered “core cells”, while grid cells with more than 30%
825 and up to 70% of component species were “intermediate cells”. Finally, grid cells with less
826 than 30% of component species were considered “marginal cells”.

827 2.3 Results

828 2.3.1 Species distribution dataset

829 Our verified point-locality database includes 340 taxa, comprising 124 amphibians,
830 129 reptiles, 45 birds, and 42 mammals, and an updated list of Cerrado endemic terrestrial
831 vertebrate species, including a synthesis of range data, is provided in [Appendix S1](#). The
832 addition of mammals and birds, as well as the inclusion of amphibians and squamates
833 described after [Azevedo et al. \(2016\)](#), added a total of 9,416 new records to our analyses,
834 totalling 13,800 unique records. To our knowledge, our point-locality database represents
835 the most reliable, detailed and comprehensive compilation of endemic vertebrate distri-
836 bution in the Cerrado. The grid system and the resulting presence-absence matrix are
837 available in [Appendix S3](#) and [Appendix S4](#), respectively.

838 2.3.2 First prediction of the vicariance model: test for clustered ranges

839 The observed T statistic (0.3065) was significantly smaller than expected by chance
840 (T varied between 0.3165 and 0.3693, with a mean of 0.3448 in 1,000 artificial populations
841 generated under null models; $p < 0.001$). This indicates that ranges of endemic terres-
842 trial vertebrates form distinguishable, non-random, regionalized biotas in the Cerrado,
843 corroborating the first major prediction of the vicariance model (see [Hausdorf & Hennig,](#)
844 [2003, 2006; Hennig & Hausdorf, 2004](#)) and detecting a significant regionalization pattern
845 for Cerrado endemic terrestrial vertebrates.

846 2.3.3 Identification of Biotic Elements

847 In the clustering analysis, 182 species (ca. 53% of the total) were assigned to 29
848 Biotic Elements ([Table 2](#)), with 158 species (ca. 46%) included in the noise component.
849 The combination of $cutdist = 0.15$ and $nnout = 2$ preserved spatial contiguity while
850 increasing the number of BEs and producing a proportion “Noise/Number of BEs” around
851 five, while requiring at least three co-distributed species to recognize a cluster. Although
852 other combinations resulted in proportions closer to 8.5 (see [Appendix S2](#)), the inclusion of
853 species with wider distributions frequently contributed to the detection of poorly delimited
854 units.

855 Biotic Elements were named according to the position of their core cells in relation
856 to major topographic units, as in [Nogueira et al. \(2011\)](#) and [Azevedo et al. \(2016\)](#). No
857 BE was formed exclusively by a single vertebrate group ([Table 2](#)). Numbers of species
858 from each terrestrial vertebrate group assigned to BEs and the noise component were not
859 significantly different from the total of analyzed species in each vertebrate group ($\chi^2 = 20$,
860 $df = 16$ $p = 0.2202$). In other words, all terrestrial vertebrate groups are proportionally

Table 2 – Range size and elevational category, total number of species, and number of species per vertebrate group within BEs. Asterisks indicate BEs detected for the first time in the Cerrado.

BE	Range size	Elevation	Total	W	P	R	Amphibians	Reptiles	Birds	Mammals
1	restricted	plateau	39	0	3	36	21	9	5	4
2	wide	general	17	14	3	0	3	2	11	1
3	restricted	plateau	13	0	0	13	10	1	0	2
4	partial	plateau	10	0	10	0	1	5	4	0
5	restricted	plateau	8	0	1	7	6	2	0	0
6	restricted	depression	7	0	0	7	3	3	0	1
7	restricted	plateau	7	0	0	7	2	5	0	0
8	restricted	plateau	6	0	0	6	5	1	0	0
9	restricted	plateau	6	0	2	4	4	1	0	1
10	restricted	depression	5	0	0	5	1	4	0	0
11	restricted	depression	5	0	2	3	0	2	1	2
12	restricted	plateau	4	0	0	4	3	1	0	0
13	partial	plateau	4	0	4	0	2	0	2	0
14	partial	plateau	4	0	4	0	0	4	0	0
15	partial	depression	4	0	3	1	1	0	2	1
16	restricted	plateau	4	0	0	4	1	3	0	0
17	restricted	depression	3	0	0	3	0	3	0	0
18	restricted	plateau	3	0	0	3	0	3	0	0
19*	restricted	depression	3	0	1	2	2	0	0	1
20	restricted	depression	3	0	0	3	1	2	0	0
21	restricted	plateau	3	0	1	2	2	0	1	0
22	partial	general	3	0	3	0	1	2	0	0
23	partial	depression	3	0	3	0	1	2	0	0
24*	restricted	plateau	3	0	0	3	2	0	0	1
25	restricted	general	3	0	0	3	0	3	0	0
26	partial	depression	3	0	2	1	2	0	1	0
27*	restricted	depression	3	0	1	2	0	2	0	1
28	partial	depression	3	0	2	1	3	0	0	0
29	partial	depression	3	1	2	0	1	2	0	0

W, P and R= number of widespread, partially distributed and restricted-range species, respectively.

prone to be assigned to the noise component or to BEs, independent of the number of species per group.

According to the predominant range size category among species in each BE, 19 units were composed mostly of restricted-range species ([Figure 6](#), see also [Table 2](#)). Only one unit was composed primarily of wide ranging species and was classified as a widespread unit ([Figure 7a](#)), with nine units composed mostly of partially-distributed species ([Figure 7b-f](#)). The list of species within each BE described above as well as in BEs detected in previous analysis can be found as [Supporting information](#) (see [Appendix S1](#)).

2.3.3.1 Restricted Biotic Elements

Most (19, 65.5%) of our BEs were geographically confined, and formed by restricted-range species. A total of 128 species, including all tetrapod groups, were assigned to these smaller units, composed mainly by amphibians (63 species), followed by reptiles (45), mammals (13) and birds (7) ([Table 3](#)). Only seven BEs had at least one partially ranged

species, with a maximum of three assigned to BE 1, composed of all groups of terrestrial vertebrates (Table 2). BE 1 was the richest unit in our analysis, with 39 species and, among restricted BEs, was followed by BE 3 (13 species) and BE 5 (8 species). Despite the high number of species in these units, 42% of the restricted BEs were composed of only three species (Table 2), indicating that restricted ranges in the Cerrado are largely allopatric.

Restricted BEs were recovered throughout the Cerrado (Figure 6), with six units found in the western portion of the region (BEs 6, 10, 11, 19, 25 and 27). Three units were concentrated on the Central Brazilian Plateau (BEs 3, 5, and 9); three in the eastern Cerrado (BEs 7, 16 and 18) and three in the southern Cerrado (BEs 8, 21 and 24). The northern portion of the region had two restricted BEs (17 and 20), and the southeastern and central western portions had one unit each. Despite some overlap at marginal and intermediate cells, most restricted BEs showed allopatric cores, except for BEs 5 and 9 which shared a core cell at the “Chapada dos Veadeiros” plateau (Figure 6). Additionally, except for the disjunct BE 9 (Figure 6b), all restricted BEs presented a continuous set of core cells.

2.3.3.2 Partial Biotic Elements

Nine (31%) of our range clusters comprised partial BEs, composed of 37 species (Table 2; Figure 7b-f). Three of these units were complementary, representing different portions of the Araguaia River basin (BEs 15, 26 and 28), while two other units shared core cells in the Upper Paraná (La Plata) basin, representing both the Southern Cerrado as a whole and the Paulistânia subregion (BEs 4 and 14 respectively). Three of the remaining units represented distinct regional portions of the Cerrado, namely: the Southeastern region (BE 13), with core cells in both the Central Brazilian Plateau and the Espinhaço range; the Tocantins basin (BE 22); and the uplands surrounding the Pantanal (BE 23). Finally, the last partial unit (BE 29) had core cells scattered from the lower Tocantins river to the western portion of the Cerrado. Partial BEs varied in terms of vertebrate composition, with reptiles and amphibians representing more than half of their component species (12 species each), followed by birds, (9 species). Most partial BEs were composed of at least two terrestrial vertebrate groups (Table 2).

Table 3 – Absolute number and approximate percentages of species composing BEs in each range-size category. Percentages are relative to the total number of species of a given group assigned to BEs. In parenthesis is the number of units per category.

	Total	Amphibians	Reptiles	Birds	Mammals
Widespread	17 - 10% (1)	3 - 4% (1)	2 - 3% (1)	11 - 41% (1)	1 - 7% (1)
Partial	37 - 20% (9)	12 - 15% (8)	15 - 24% (5)	9 - 33% (4)	1 - 7% (1)
Restricted	128 - 70% (19)	63 - 81% (14)	45 - 73% (16)	7 - 26% (3)	13 - 87% (8)

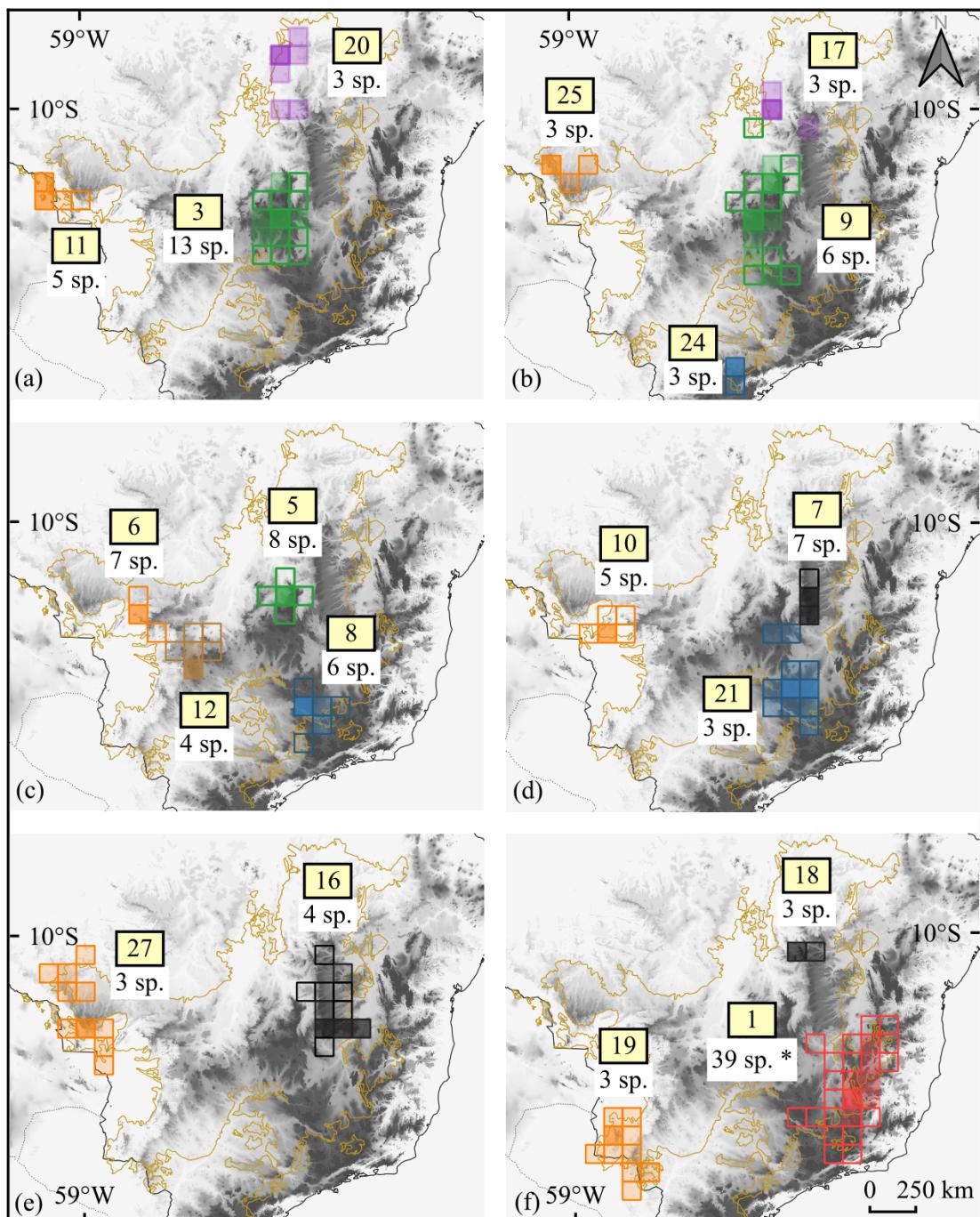


Figure 6 – Restricted-range Biotic Elements (BEs) composed of endemic terrestrial vertebrates in the Cerrado (limits represented by the yellow line). BEs named according to major topographic units or as in Azevedo et al. (2016) for BEs composed of at least 50% of the same species in both studies: (a) 3 - Central Brazilian plateau - Brasília nucleus; 11 - Huanchaca plateau/Guaporé River valley; 20 - Lower Tocantins River valley. (b) 9 - Central Brazilian plateau - Serra dos Pirineus nucleus; 17 - Middle Tocantins River valley; 24 - Campos Gerais (Paraná state); 25 - Parecis plateau. (c) 5 - Serra da Mesa/Veadeiros plateau. 6 - Guimarães plateau. 8 - Canastra plateau. 12 - Caiapônia plateau. (d) 7 - Serra Geral plateau. 10 - Serra das Araras/Paraguay-Jauquara basin. 21 - Upper Paranaíba region. (e) 16 - Upper São Francisco River; 27 - Parecis Plateau/Upper Guaporé River valley. (f) 1 - Espinhaço Mountain Range; 18 - Jalapão; 19 - Bodoquena. Asterisks indicate BEs composed of all groups of terrestrial vertebrates. Elevation is divided into four shades of grey, with the two lighter shades representing 0-250 and 250-500 m respectively, and the darker representing 500-750, 750-1,000, and above 1,000 m. The contrast between the lighter and darker shades highlights the threshold separating “Plateau” from “Depression” units (see Silva, 1997). Numbers in yellow squares are the BE number. The number of species (sp.) in each unit is below the BE number.

904 2.3.3.3 *Widespread Biotic Element*

905 We detected only one Biotic Element (BE 2) composed primarily of widespread
906 species ([Figure 7a](#)). BE 2 included 17 species from all groups of terrestrial vertebrata
907 tes ([Table 2](#)). Birds were predominant in this BE (11 species), followed by amphibians
908 (3), reptiles (2) and mammals (1). The core and intermediate cells were scattered th-
909 roughout the Cerrado. Typical, widespread Cerrado vertebrate species compose this unit,
910 including the amphibians *Physalaemus nattereri* (Steindachner, 1863) and *Chiasmocleis*
911 *albopunctata* (Boettger, 1865); the reptiles *Bothrops moojeni* Hoge, 1966 and *Epicrates*
912 *crassus* Cope, 1862, the birds *Antilophia galeata* (Lichtenstein, 1823), *Melanopareia tor-*
913 *quata* (Wied, 1831) and *Saltatricula atricollis* (Viellot, 1817), and the mammal *Lycalopex*
914 *vetulus* (Lund, 1842).

915 2.3.4 *Second prediction of the vicariance model: are closely related species
916 found in different BEs?*

917 The chi-squared test failed to reject the null hypothesis that closely related species
918 are scattered among Biotic Elements ($\chi^2 = 2589.3$, $df = NA$, $p = 0.7737$). It means that
919 congeneric species were generally found in distinct BEs, giving support to the second ma-
920 jor prediction of the vicariance model: allopatric ranges of closely related taxa as a result
921 of biogeographical barriers ([Hausdorf & Hennig, 2006](#)). The genera with most species
922 forming BEs were the amphibians in *Scinax* (12 species in seven BEs), *Bokermannohyla*
923 (nine in five), *Boana* (eight in seven), *Proceratophrys* (seven in five), *Physalaemus* (six in
924 three), *Rhinella* (four in four) and the reptiles in *Amphisbaena* (nine in seven); *Aposto-*
925 *lepis* (six in six); *Bachia* (four in four), *Tropidurus* (five in four) and *Phalotris* (four in
926 three, see [Appendix S1](#)).

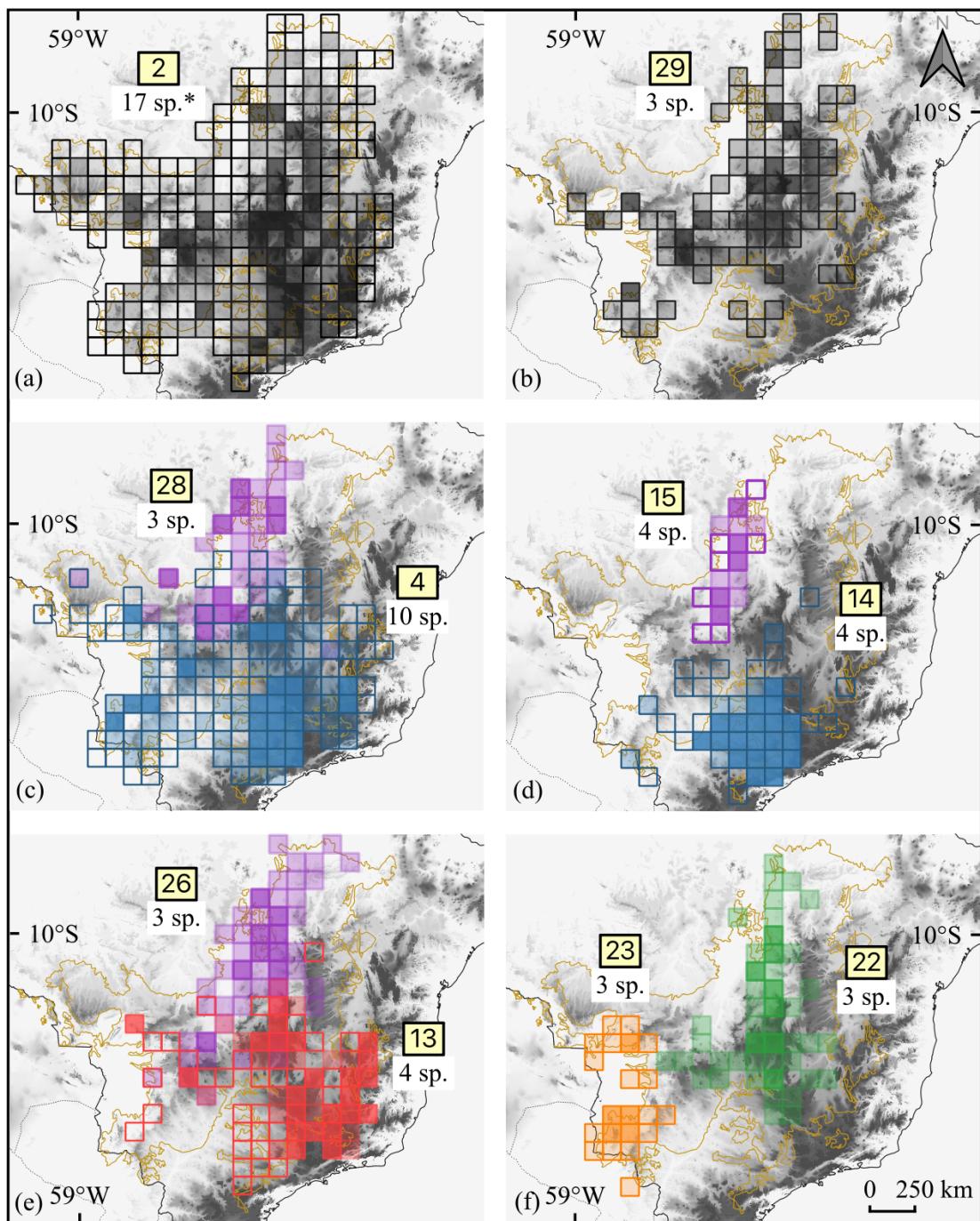


Figure 7 – Widespread and Partial Biotic Elements (BEs) composed of endemic terrestrial vertebrates in the Cerrado (limits represented by the yellow line). Biogeographical units named according to the overall region occupied by intermediate cells (>30% of the component species), core cells (>70% of the component species) and the major topographic units, when possible: (a) 2 - Whole Cerrado. (b) 29 - Northwestern Cerrado. (c) 4 - Southern Cerrado/Upper Paraná (La Plata) basin; 28 - Roncador Range/Araguaia basin. (d) 14 - Paulistânia/Upper Paraná (La Plata) basin; 15 - Middle Araguaia River valley. (e) 13 - Southeastern Cerrado; 26 - Araguaia basin. (f) 22 - Tocantins basin; 23 - Pantanal/Upper Paraguay basin. Asterisks indicate BEs composed of all groups of terrestrial vertebrates. Elevation is divided into four shades of grey, with the two lighter shades representing 0-250 and 250-500 m respectively, and the darker representing 500-750, 750-1,000, and above 1,000 m. The contrast between the lighter and darker shades highlight the threshold separating “Plateau” from “Depression” units (see Silva, 1997). The numbers in the yellow squares are the BE number. The number of species (sp.) in each unit is below the BE number.

927 2.3.5 *Elevation and BEs*

928 The elevational range of all unique species records varied from zero to 2,067 m,
 929 with a median of 611 m. Species from plateaus or depressions tended to compose the
 930 same elements ($\chi^2 = 198.45$, $df = \text{NA}$, $p < 0.001$, for all species forming BEs, and $\chi^2 =$
 931 121.04, $df = \text{NA}$, $p < 0.001$ for species forming restricted BEs only), corroborating the
 932 hypothesis that altitudinal isolation may be an important driver of Cerrado endemism
 933 and regionalization patterns (Figure 8). Based on the distribution of elevation records,
 934 we found 14 Plateau BEs, 12 Depression BEs and three general BEs (see Table 2 and
 935 Figure 8).

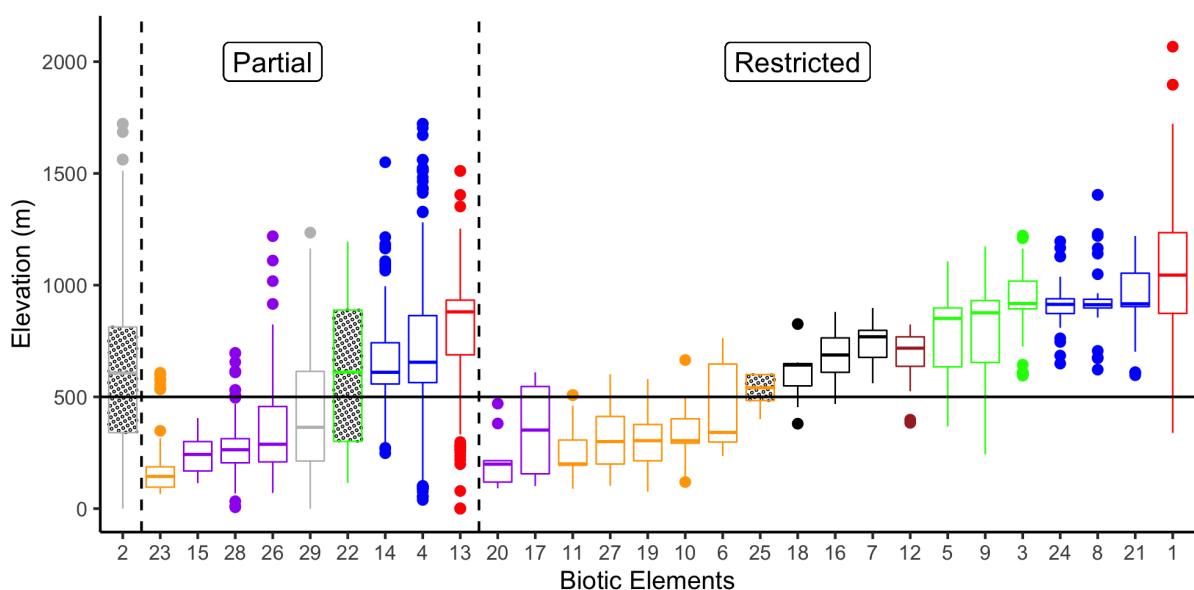


Figure 8 – Elevation range of Biotic Elements formed by endemic terrestrial vertebrates in the Cerrado. Boxes represent the interquartile range (IQR: Q1 - 25 percentile and Q3 - 75 percentile), composing 50% of all elevational records. The line of central tendency is the median. Whiskers represent “Maximum” (Q3 + 1.5*IQR), and “Minimum” (Q1 - 1.5*IQR). The points above or below the whiskers are outliers. Units are coloured as in Figure 6 and Figure 7 and according to general geographical position in the Cerrado (e.g. Northern - Purple; Central western - Brown; Western - Orange; Central - Green; Eastern - Black; Southern - Blue; Southeastern - Red). The horizontal line represents the threshold separating “Plateau” from “Depression” units (see Silva, 1997). “General” Biotic Elements are filled with circles (see Appendix S1).

936 Biotic Elements with the lowest values of elevation are concentrated in the western
 937 portion of the Cerrado, near contacts with Amazonia and wetlands of the Paraguay or
 938 Guaporé/Itenez drainages. BEs presenting the highest altitudinal ranges are located in
 939 central and southeastern portions of the Cerrado, at the core of the Brazilian Shield.
 940 Among partial BEs, all but BE 22 could be assigned to an elevation category, despite
 941 the high elevational variability within those units (Figure 8). Similarly, all restricted BEs
 942 except BEs 25, could be assigned to one of the elevational categories proposed above
 943 (Figure 8).

Table 4 – Absolute number and approximate percentages of species composing restricted BEs in each elevational category. Percentages are relative to the total number of species of a given group assigned to BEs. In parenthesis the number of units per category.

	Total	Amphibians	Reptiles	Birds	Mammals
Plateau	93 - 76% (10)	56 - 89% (10)	23 - 59% (8)	6 - 86% (2)	8 - 62% (4)
Depression	29 - 24% (7)	7 - 11% (4)	16 - 41% (6)	1 - 14% (1)	5 - 38% (4)

We found no statistical differences in number of species per vertebrate group in BEs from different elevational categories ($\chi^2 = 15$, $df = 12$, $p = 0.2414$), indicating that all vertebrate groups are equally prone to form plateau or depression units. However, for restricted BEs (units with the smallest elevational variability), amphibians and birds were much more frequent in plateau units (89% and 86% of the species, respectively), while the remaining groups were almost evenly distributed in both categories, despite the general prevalence of species in plateau units (Table 4).

2.4 Discussion

Our results, based on an extensive revised point locality database, revealed congruent endemism patterns for Cerrado terrestrial vertebrates, and detected non-random clusters of co-distributed species. The fact that all terrestrial vertebrate groups were proportionally prone to be assigned to BEs or to the noise component, independent of the number of species per group (see Table 3), indicates that no idiosyncratic trait (range size; dispersal ability) has influenced the presence of different terrestrial vertebrate groups in the recovered BEs. These multi-taxon range clusters represent significantly segregated biotas separated by altitudinal compartments (plateaus x depressions), corroborating previous hypotheses on the role of geomorphological changes as major determinants of Cerrado endemism (K. S. Brown & Gifford, 2002; Nogueira et al., 2011; Silva, 1997). Indeed, vicariant isolation in depressions and plateaus along the Brazilian shield as a result of Neogene orogeny has been pointed as the most plausible explanation for genetic divergence in the frog genus *Dermatonotus*, widespread in central portions of South America (E. F. Oliveira et al., 2018).

However, corroborating major predictions of the vicariant model does not prove that the recovered pattern was indeed a result of vicariance (Hausdorf, 2002). Vicariant scenarios could be further tested using timed phylogenies and biogeographical barriers, under explicit historical biogeographical analyses (Hausdorf, 2002; Hennig & Hausdorf, 2004). Biotic Elements are the primary spatial units, or necessary first step, to test if the recovered patterns were formed in response to the same general historical events/barriers or a result of secondary dispersal or similar processes (Hausdorf, 2002). Whether or not a direct result of vicariance, species forming BEs share the same areas, representing, at least,

non-random, non-arbitrary geographical units, objectively derived from raw distribution data ([Hausdorf, 2002](#)).

The regionalization pattern recovered herein corroborates and complements results based on data for the Cerrado herpetofauna ([Azevedo et al., 2016](#); [Nogueira et al., 2011](#)) and supports the hypothesis that repeated and congruent patterns may be general and ruled by the same major scale determinants. Six out of seven units in [Nogueira et al. \(2011\)](#) and 13 out of 16 in [Azevedo et al. \(2016\)](#) were also recovered based on our terrestrial vertebrate dataset. Only three BEs (“Chapada das Mesas”, “Serra da Borda” and “Roncador plateau”) detected by [Azevedo et al. \(2016\)](#) were not recovered in the present study, and their component species were assigned to the noise component in our analyses. Moreover, some species assigned to these previous units were not included in our analysis due to taxonomic changes or uncertainties ([Frost, 2020](#); [Uetz et al., 2020](#)). On the other hand, units such as BE 19 (“Bodoquena”), BE 24 (“Campos Gerais, Paraná state”) and BE 27 (“Upper Guaporé Valley”) had never been detected before, indicating that Linnean and Wallacean shortfalls posed limitations for our understanding of biogeographical patterns and processes in the Cerrado. Some of the BEs detected here represent smaller portions of previously detected larger units. For example, the “Paraguay-Guaporé” unit of [Nogueira et al. \(2011\)](#) was split into the “Serra das Araras/Paraguay-Jauquara basin” (BE 10), “Huanchaca plateau/Guaporé River valley” (BE 11), and “Parecis plateau” (BE 25) units (see [Appendix S1](#)). This refinement indicates that taxonomically diverse datasets increase the potential to unravel previously overlooked biogeographical patterns while also providing support and more detail for well-established biogeographical units.

Furthermore, most of the ten floristic provinces detected for Cerrado endemic species of the plant genus *Mimosa* ([Simon & Proença, 2000](#)) are congruent with BEs detected for endemic terrestrial vertebrates, including the “Western Cerrado”, “Southern Cerrado”, “Serra do Espinhaço South”, “Serra do Espinhaço North”, “Central Western Cerrado” and “Central Highlands” provinces. Additionally, the cores of BEs 4, 15, and 23, as well as the restricted BE 5, are partially congruent, respectively, to the floristic districts “South”, “North-West”, “South-West”, and “Central” proposed by [Françoso et al. \(2020\)](#). These large phytogeographical units, however, fail to detect and describe more detailed internal complex endemism patterns, and generally correspond to our partial BEs. Moreover, these linearly defined, perfectly allopatric districts (as most traditional biogeographical units, see [Hausdorf, 2002](#)), fail to account for peripheral contact and partial sympatry that are characteristic of raw distribution data, and that may be typical of natural, data-driven biogeographical units ([Hausdorf, 2002](#)).

The high proportions of amphibians, reptiles and mammals in restricted BEs indicates that these groups might respond similarly to biogeographical drivers, as opposed to birds, that were proportionally richer in widespread or partial BEs (see [Table 3](#)). Birds have the largest geographical distributions among vertebrates ([Gaston, 1996](#)), and

their high mobility (Sick, 1997) may mask patterns originated by vicariance due to post-speciation dispersal (Hausdorf, 2002). The fact that birds were richer in widespread BEs, while relatively rare in partial or restricted BEs, may be a result of this greater dispersion capacity and relatively wide ranges. However, birds were still important components of most recovered BEs, especially in plateau units, indicating that dispersal has not fully erased significant regionalization patterns in this group. In fact, three of the four areas of avian endemism for the Cerrado proposed by Silva (1997) were recovered as BEs: “Espinhaço Plateau” = Espinhaço mountain range” - BE 1, “Araguaia River Valley” = Araguaia River basin” - BE 15, and “Central Goiás Plateau” = “Upper Parnaíba region” - BE 21.

Depression units showed the lowest number of species in their composition, corroborating the idea that endemism predominates along isolated plateaus (Nogueira et al., 2011). However, the western portion of the Cerrado, where most depression units are concentrated, is markedly less explored (see U. Oliveira et al., 2016), and therefore, may harbour important areas for further surveys and species taxonomic assessment. For instance, two out of seven restricted depression units are novel BEs, and four are fine-scale splits from larger, previously detected units. This suggests that systematic regional fieldwork is still necessary to test the units proposed here and to unravel finer scale biogeographical units.

Although most BEs showed a predominant elevation range type (plateaus/depressions), most were formed both by plateau and depression species. This indicates that topographical changes, possibly generated by major tectonic shifts along the Miocene and Pliocene (see E. F. Oliveira et al., 2018; Silva, 1997; Teixeira Jr. et al., 2016, and references therein) may have acted simultaneously on the isolation of fragmented plateaus and disconnected depressions, interpreted as mutual “soft” barriers (see Teixeira Jr. et al., 2016). These major continental topographical changes are now reflected in the Cerrado complex endemic faunas, regionalized according to conspicuous Cerrado topographical units, including the central Brazilian Plateau, Chapada dos Guimarães plateau, Parecis plateau, Paraguay depression, Espinhaço range, Araguaia and Tocantins depression, among many others, which largely correspond to the major subdivisions of the Brazilian shield (Silva, 1997). The complex and nested pattern shown by these units (see Figure 6) suggests that multiple and sequential topographical changes have successively fragmented and shaped ranges in the Cerrado (see Nogueira et al., 2011; Silva, 1997; Vasconcellos et al., 2019).

Although previous phylogeographical analyses (Lima-Rezende et al., 2019; Santos, de Campos Nogueira, Giugliano, & Colli, 2014; Vasconcellos et al., 2019) did not recognize distinct species within the widespread taxa analysed, they point to a strong genetic structure coincident with some of our proposed units. Santos et al. (2014), for instance, revealed three major genetic units for the Cerrado endemic lizard *Micrablepharus atticolus* Rodrigues 1996 corresponding roughly to our BEs 4, 29 and 26, respectively. Future phylogeographical studies may consider our results relevant to the interpretation of their

1052 findings, as we predict that ranges of cryptic species within widespread taxa may be
1053 congruent with our biogeographical units (see [Vasconcellos et al., 2019](#)). Similarly, BEs
1054 would also aid in delimiting ranges of poorly studied or newly described species and by
1055 providing significant boundaries to range predictions in species distribution modelling
1056 ([Franklin, 2010](#); [Raxworthy et al., 2003](#)).

1057 As Biotic Elements analysis detects multiple regionalized biotas, providing support
1058 to allopatric speciation and vicariance ([Azevedo et al., 2016](#); [Hausdorf & Hennig, 2003](#);
1059 [Nogueira et al., 2011](#); present study), we posit that new species descriptions in the Cerrado
1060 will tend to replicate the spatial patterns detected for terrestrial vertebrates (which, in
1061 turn, largely coincides with floristic endemism, see [Simon & Proen  a, 2000](#)). Our broad
1062 regionalization patterns may serve as a template for the discovery of new species (and
1063 biogeographical patterns) in less studied groups such as fishes and invertebrates. We may
1064 be approaching a consensus on the regionalization of the richest and most threatened
1065 savanna of the planet. Further analyses incorporating a more inclusive and representative
1066 taxonomic dataset should provide robust tests for this hypothesis. The inclusion of recent
1067 data on species ranges and endemism resulted in the discovery of novel biogeographical
1068 patterns already under threat in the light of the rapidly changing land use scenario in
1069 central Brazil ([Liu, Slik, Zheng, & Lindenmayer, 2022](#); [Strassburg et al., 2017](#)).

1070 Topographical differences between plateaus and depressions were interpreted as ma-
1071 jor drivers of past climatic stability in central Brazil, with plateaus pointed as climatic
1072 refugia in Pleistocene climate shifts, conserving stable savanna/gallery forest mosaics over
1073 time ([K. S. Brown & Gifford, 2002](#); [Vasconcellos et al., 2019](#)). Moreover, plateaus in the
1074 Serra Geral (BE 7) and Espinha  o Range (BE 1) were pointed as potential Cerrado re-
1075 fugia in past climatic fluctuations ([Werneck, Nogueira, Colli, Sites, & Costa, 2012](#)). In
1076 fact, many restricted BEs were associated with eastern highland plateaus, which might
1077 support the idea that climatic stability (even though only indirectly, see [Marin et al.,](#)
1078 [2018](#)) and topography were important for the origin of Cerrado endemic species ([Lima-](#)
1079 [Rezende et al., 2019](#); [Silva, 1997](#); [Vasconcellos et al., 2019](#)). Moreover, if past climate
1080 refugia were concentrated on plateaus ([Werneck et al., 2012](#)), most of our restricted BEs
1081 may represent critical areas for conserving biotas under climate change scenarios. These
1082 areas were important for the history of Cerrado endemic biotas and may also be critical
1083 for their conservation in an uncertain future.

1084 Our results indicate that the origin, history and fate of biogeographical units in
1085 the Cerrado seem highly connected to historical landscape changes and topographical
1086 complexity, in agreement with previous studies ([Nogueira et al., 2011](#); [Silva & Bates,](#)
1087 [2002](#)). We also highlight the importance of revised point-locality databases, incorporating
1088 planned inventories and accumulated revised voucher specimens as a critical first step for
1089 biogeographical analyses and biodiversity syntheses (see [Hausdorf, 2002](#); [Nogueira et al.,](#)
1090 [2019](#)). Our general, detailed and complex bioregional patterns, including narrow ranged,

1091 recently described and highly irreplaceable biotas, can be decisive to inspire broader
1092 discussions on the origin and destiny of endemism in the richest and most threatened
1093 savanna on the planet.

1094 2.5 Supporting information

1095 Appendix S1

1096 List of endemic terrestrial vertebrates composing each Biotic Element (BE) or Noise
 1097 component in the Cerrado, and a description of ranges and BEs according to range extent
 1098 and topographical position in the Cerrado. BEs previously detected as composed of
 1099 a given species in [Nogueira et al. \(2011\)](#) and [Azevedo et al. \(2016\)](#) are also provided.
 1100 Appendix S1 is provided in .xlsx format.

1101 Appendix S2

Combinations of the parameters *cutdist* and *nnout* compared for the detection of Biotic Elements through hierarchical clustering in package ‘prabclus’. The value of *k* with our dataset is 8.5. **Bold** values are the combination choosen to map Biotic Elements. Green backgrounds are all combinations with previzualized and compared results.

	Cutdist	0.1	0.15	0.2	0.25	0.3	0.35	0.4	0.45	0.5
nnout = 1	Noise	175	112	56	28	10	5	4	1	1
	BEs	50	52	52	43	31	27	21	13	11
	Prop	3.5	2.15	1.08	0.65	0.32	0.19	0.19	0.08	0.09
nnout = 2	Noise	233	158	96	52	18	15	12	3	1
	BEs	21	29	32	31	27	22	17	12	11
	Prop	11.1	5.45	3	1.68	0.67	0.68	0.71	0.25	0.09
nnout = 3	Noise	260	197	114	73	30	24	15	6	4
	BEs	12	16	26	24	23	19	16	11	10
	Prop	21.67	12.31	4.38	3.04	1.3	1.26	0.94	0.55	0.4
nnout = 4	Noise	280	217	142	85	42	32	23	6	4
	BEs	7	11	19	21	20	17	14	11	10
	Prop	40	19.73	7.47	4.05	2.1	1.88	1.64	0.55	0.4
nnout = 5	Noise	290	227	162	95	47	37	28	6	4
	BEs	5	9	15	19	19	16	13	11	10
	Prop	58	25.22	10.8	5	2.47	2.31	2.15	0.55	0.4

1102 Appendix S3

1103 Grid system ($1^{\circ} \times 1^{\circ}$) used in the Biotic Element analysis, based on the Cerrado
 1104 ecoregion limits proposed by [Dinerstein et al. \(2017\)](#) with the same grid origin as used
 1105 in [Azevedo et al. \(2016\)](#). Appendix S3 is provided in .zip format including .shp and
 1106 supporting files.

1107 Appendix S4

1108 Presence-absence matrix based on the intersection of verified point-locality records
 1109 and the grid system provided as Appendix S3 in Supporting Information. Lines are
 1110 species; columns are grid cells, column names are grid cells “ID”. Appendix S4 is provided
 1111 in .csv format.

1112 3 How habitat loss and fragmentation are 1113 reducing conservation opportunities for vertebrates in the most threatened savanna of the World

1113

Abstract

1114 Effective, resilient and strategic protected area networks are essential to protect biodiver-
1115 sity and human welfare, especially in vulnerable biodiversity hotspots. This is the case in
1116 the Brazilian Cerrado, the richest tropical savanna, and a deforestation front worldwide.
1117 Worryingly, the rate of habitat conversion in Cerrado greatly reduces opportunities to
1118 conserve its biodiversity. Herein, using the most comprehensive database on the distri-
1119 bution of Cerrado endemic terrestrial vertebrates, we mapped conservation priority areas
1120 and evaluated how and to what extent habitat loss and fragmentation reduce conservation
1121 opportunities. Priority areas are scattered throughout the Cerrado. Larger priority areas
1122 are concentrated in the northern portion of the region. Southern priority areas are small,
1123 scattered, and isolated. During the last 35 years, opportunities to conserve large con-
1124 tiguous areas have significantly decreased, hampering the representation of key endemic
1125 species. However, as most endemic vertebrates are small ranged, modest but well located
1126 increments in total protected area will result in significant overall improvements in the
1127 PA system. Protecting the largest priority areas identified here is urgent and mandatory,
1128 while using habitat restoration as a key activity to promote connectivity among smaller
1129 priority areas, especially in the southern portion of this hotspot.

1130 **Keywords:** Cerrado biodiversity hotspot; Conservation planning; Deforestation hots-
1131 pots; Endemism; Habitat fragmentation; Terrestrial vertebrates

1132 3.1 Introduction

1133 Creating and managing strategic protected areas (PAs) is fundamental for biodiver-
1134 sity conservation. They are essential to reaching nature-based solutions for adaptation to
1135 global changes (Maxwell et al., 2020), maintaining wildlife populations (Geldmann et al.,
1136 2013), and ensuring long-term maintenance of nature's contributions to people (Díaz et
1137 al., 2018). Worryingly, despite the sustained increase in numbers of PAs globally (Maxwell
1138 et al., 2020), historically PA allocation has not met scientific criteria, being influenced
1139 by economic activities and opportunism (Margules & Pressey, 2000). This is particularly
1140 true in economically productive ecoregions (Prieto-Torres et al., 2022) such as the Cerrado
1141 hotspot (Strassburg et al., 2017; Vieira, Pressey, & Loyola, 2019). In this context, science
1142 has developed systematic conservation planning protocols to achieve resilient and effective
1143 PAs, based on objective criteria and relevant information (Di Minin, Veach, Lehtomäki,
1144 Pouzols, & Moilanen, 2014; Margules & Pressey, 2000).

1145 Habitat loss and fragmentation are the main causes of species extinctions and de-
1146 clines, hampering population viability of most threatened species (Grande et al., 2020;
1147 IPBES, 2019). Conservation opportunities for efficient PAs exponentially decrease as ha-
1148 bitat fragmentation advances (Nori et al., 2013). The protection of contiguous patches of
1149 natural ecosystems is necessary for the conservation of most key and threatened species,
1150 ecological processes, and nature's contributions to people (Díaz et al., 2018). Sadly, cur-
1151 rent rates of conversion of the few remaining natural habitats in deforestation hotspots,
1152 such as the Brazilian Cerrado, make this unlikely.

1153 The Brazilian Cerrado is the richest savanna in the world, with high levels of ende-
1154 mism (Strassburg et al., 2017). However, this biodiversity hotspot has recently suffered
1155 rampant natural habitat loss due to a combination of low legal protection and increased
1156 demand for commodities (P. Pacheco et al., 2021). Additionally, the Cerrado is one of
1157 the eight deforestation frontiers undergoing high rates of recent deforestation, with con-
1158 version now concentrated in the northern portion of the region, where natural habitats
1159 persist as large contiguous areas (Strassburg et al., 2017). Given the context, efficient
1160 policy-making toward their conservation is imperative.

1161 Herein, using the most comprehensive revised point-locality database on endemic
1162 terrestrial vertebrates of the ecoregion to date, we aimed (i) to determine priority areas for
1163 the conservation of Cerrado endemic terrestrial vertebrates; (ii) to determine the increase
1164 of habitat fragmentation of priority areas as the agricultural frontier advances; and (iii)
1165 to estimate the loss of conservation opportunities over time under current deforestation
1166 rates.

1167 3.2 Materials and Methods

1168 *Disclaimer*

1169 No artigo original ([Vieira-Alencar et al., 2023](#)), o texto publicado contém uma versão
1170 reduzida dos materiais e métodos desse trabalho e adicionamos um apêndice ao material
1171 suplementar do artigo, nomeado *Extended methods*. No entanto, aqui na tese optei por
1172 apresentar diretamente a versão completa dos materiais e métodos.

1173 3.2.1 *Study area*

1174 The Cerrado is the second largest South American phytogeographical domain, sur-
1175 passed in extension only by Amazonia and occupying a central position in the Neotropical
1176 region, being dominated by upland savannas and grasslands ([Ab'Sáber, 1998](#)). It is borde-
1177 red in the northwest by the Amazon and in the east by the Atlantic Forest, and forms the
1178 South American diagonal of open vegetation together with the Caatinga in the northeast
1179 and the Gran Chaco in the southwest. This savanna ecoregion is dominated by hetero-
1180 geneous xeromorphic vegetation ranging from areas dominated by grasslands, with small
1181 shrubs (campo limpo), to areas formed by almost closed canopy woodland (cerradão;
1182 [Eiten, 1972](#); [Ratter et al., 1997](#)). However, the Cerrado has been intensively modified
1183 by the conversion of its natural vegetation into croplands and planted pastures, which
1184 implies deforestation rates higher than the Amazon, coupled with less legal protection of
1185 its outstanding endemic biodiversity ([Strassburg et al., 2017](#)).

1186 We adopted the limits of the Cerrado ecoregion as proposed by [Dinerstein et al.](#)
1187 ([2017](#)), which is an ecoregion approach initially based on the Cerrado limits of the Ins-
1188 tituto Brasileiro de Geografia e Estatística ([IBGE, 1993](#); see [Olson et al., 2001](#)). As we
1189 included a variable containing land use information, available mainly for the Brazilian ter-
1190 ritory ([MapBiomass, 2022](#); see below), we retained the Brazilian portion of the ecoregion
1191 corresponding to 99.23% of the Cerrado, after removing its small portions in Paraguay
1192 and Bolivia.

1193 3.2.2 *Species and occurrence records*

1194 Our database is composed of 13,790 unique records of 337 Cerrado endemic terres-
1195 trial vertebrates, including 124 amphibian anurans, 66 lizards, 63 snakes, 45 birds and
1196 39 mammals, with a mean of 2,758 distribution records per group ($sd = 2,097$), and a
1197 mean of 41 records per species ($sd = 93$). This is the most comprehensive database of
1198 geographic information on Cerrado endemic terrestrial vertebrates to date. These records
1199 are based on planned field surveys to cover previous sampling gaps and revision of vouche-
1200 red specimens deposited in scientific collections (see details in [Carmignotto et al., 2022](#);
1201 [Nogueira et al., 2019, 2009; Valdujo et al., 2012](#)), complemented by revised literature

1202 data. We considered endemic species, those with ranges fully or largely coincident with
1203 the approximate limits of the Cerrado provided in Dinerstein et al. (2017). Species with
1204 marginal records in transitional areas between the Cerrado and other domains, but with
1205 local ranges associated with typical environments of the Cerrado were also considered
1206 endemic, due to their possible historical association to once continuous areas of Cerrado.
1207 The nomenclature follows specific literature for each vertebrate group (Frost, 2020 for
1208 anurans, Uetz et al., 2020 for lizards/amphisbaenians, Nogueira et al., 2019 for snakes,
1209 J. F. Pacheco et al., 2021 for birds, and Abreu et al., 2021 for mammals).

1210 We departed from verified point-locality records and created normalized heatmaps
1211 to represent species distributions. Heatmaps represent a simple extrapolation of a spe-
1212 cies point occurrence, highlighting regions with a high density of records and giving less
1213 weight to pixels towards the edge of the buffered heat core. The highest values are attri-
1214 buted to the exact location where the species was recorded and lower values are continu-
1215 ously attributed to pixels further away from the verified occurrence (QGIS Development
1216 Team, 2022a). This approach allows us to give relatively less importance to pixels dis-
1217 tant from the original species record without disregarding the potential of surrounding
1218 areas to contain suitable environmental conditions for a given species. Also, compared
1219 with other commonly used methods based on correlative extrapolations, and considering
1220 the completeness of our database, heatmaps are only based on the distributional records,
1221 minimizing potential commission errors as a consequence of spurious projections. Finally,
1222 using heatmaps avoids overlooking potentially important areas around a species record
1223 (e.g. decreasing the effect of omission errors) while also dealing with putative commission
1224 errors by decreasing the importance of a pixel according to its distance from the verified
1225 occurrence.

1226 We created the heatmaps using the Kernel Density Estimation tool, available in
1227 QGIS 3.24 (QGIS Development Team, 2022b). In order to create a spatially representative
1228 extrapolation we defined the radius of 0.5° providing a 1° circular area around the species
1229 record. In the Cerrado, $1^{\circ} \times 1^{\circ}$ grid systems have been used in studies on vertebrates
1230 diversity and historical biogeographical patterns (e.g. Azevedo et al., 2016; Diniz-Filho,
1231 Bini, Pinto, et al., 2008), and prioritization analyses for conservation purposes (Diniz-
1232 Filho, Bini, Vieira, et al., 2008). We used the resolution of $\sim 20\text{km}^2$ (0.041667°) and grid
1233 origin based on the WorldClim 2.5 arc minutes bioclimatic database (Fick & Hijmans,
1234 2017), to allow further comparative analyses that might consider those climatic variables
1235 (see for example Lemes, Andrade, & Loyola, 2020) and to guarantee a spatial resolution
1236 that would optimize computational requirements without excessively downgrading land
1237 use variables. We normalized the estimated heat values by dividing the resulting raster
1238 file by the maximum value of the raster, therefore obtaining a continuous output from
1239 zero to one for all species.

1240 3.2.3 Estimation of Priority Areas

1241 We used Zonation 4.0 ([Moilanen et al., 2014](#)) to identify priority areas for the conser-
1242 vation of Cerrado endemic terrestrial vertebrates. The software implements hierarchical
1243 prioritization of areas based on the distribution of biodiversity features (e.g. species,
1244 ecosystem services) considering predefined user input weights for each feature. In this
1245 case, each pixel contains information on the occurrence of a given biodiversity feature,
1246 and the algorithm continuously removes pixels with smaller values of the features of in-
1247 terest, progressively recalculating the importance of the remaining pixels and repeating
1248 this procedure until the last pixel in the study area is removed. Then, the pixels are hie-
1249 rarchically classified and the output of highly important areas can be displayed according
1250 to user-defined conservation thresholds.

1251 Zonation allows for different “cell-removal rules”. Prioritizations were run under the
1252 *Core Area Zonation* (CAZ) rule. In short, the CAZ rule identifies high-priority areas as
1253 those that present a high occurrence level of a single rare or highly weighted feature (for a
1254 more detailed explanation on different prioritization rules see [Di Minin et al., 2014](#)). This
1255 removal rule was selected given that selected input species are endemic to the Cerrado, and
1256 many are restricted to small portions of the study region. In this sense, Zonation is more
1257 likely to create an output that represents all species highlighting portions of the Cerrado
1258 that must be preserved to protect highly irreplaceable biodiversity features. To select areas
1259 optimal for expanding the PA network, we included existing PAs as a hierarchical mask ([Di](#)
1260 [Minin et al., 2014](#)). This approach leads to minimum costs to achieve conservation targets
1261 as it selects the best part of the landscape surrounding existing PAs, which are preferably
1262 retained as the first option in the analysis. The shapefile of PAs was downloaded from the
1263 World Database on Protected Areas ([IUCN & UNEP, 2020](#)) and cropped to the limits
1264 of the Cerrado. We included all PA categories, with strict and non-strict conservation
1265 goals, such as National and State Parks, Ecological Stations, and Private areas such as
1266 “APAs” and “RPPNs”, in our analysis. Only PAs with detailed geographic information
1267 were considered, excluding those represented only as a point locality.

1268 Zonation accounts for feature-specific weights prioritizing the protection of highly
1269 weighted biodiversity features (in this case species), which allows us to adapt the priori-
1270 tization to our specific aims. To emphasize the importance of microendemic, threatened
1271 (VU, EN, CR) or poorly known (DD) taxa as a precautionary measure (see [Nori, Villalo-](#)
1272 [bos, & Loyola, 2018](#)), we generated a simple index including both categories: distributional
1273 pattern and extinction risk. Our weighted index is the result of a multiplication of values
1274 from 1 to 3 (“widespread” = 1, “partial” = 2, and “restricted” = 3, see [Nogueira et al.,](#)
1275 [2019](#)) for range size, and values from 1 to 5 according to the IUCN categories (LC = 1,
1276 NT = 2, VU and DD = 3, EN = 4 and CR = 5; [IUCN, 2022](#)). Additionally, DD species
1277 described since 2010 and species currently not assessed by IUCN received the value of “2”
1278 in the extinction risk part of the index. This value represents a lower weight than weights

1279 assigned to species that remained classified as DD even after a decade of their description,
1280 while also represents a higher weight than that of taxa indisputably regarded as “Least
1281 Concern” for conservation purposes. The endemic rodent *Juscelinomys candango* was not
1282 included in the analysis because according to IUCN it is classified as extinct.

1283 In order to penalize pixels covered by anthropic land-uses, we included reclassified
1284 binary land-use maps (obtained from [MapBiomas, 2022](#)) as a negative variable with a
1285 strong weight (equal to the sum of all positive variables weights). These rasters preclude
1286 or minimize the possibility to assign a high conservation value to pixels covered by crops
1287 or urban areas (see details of the raster reclassification in the [Supporting information -](#)
1288 [Appendix S1](#)). To assess how priority areas (and conservation opportunities) have changed
1289 as a result of land use and land cover (LULC) changes throughout the last decades, we
1290 repeated the analyses using land-use map scenarios from 1985 to 2020 ([MapBiomas, 2022](#))
1291 in intervals of five years and also considered a pristine Cerrado scenario (e.g. without any
1292 LULC changes). To simulate a “pristine Cerrado scenario” we classified the whole Cerrado
1293 area as “Natural”, so no pixel was down-weighted due to the presence of anthropic uses.

1294 According to the Aichi Biodiversity Targets ([CBD, 2010](#)), protected area networks
1295 should represent at least 17% of the world’s landmass (see Target 11; [CBD, 2010](#)). We
1296 also mapped a recently proposed threshold of 30%, for the post-2020 global biodiversity
1297 framework ([Woodley et al., 2019](#)). Finally, to analyze the effect of LULC changes and
1298 resulting fragmentation on priority areas across time, we grouped patches of priority areas
1299 (i.e. connected pixels of the top 17% of priority areas in each scenario) depending on their
1300 area. We used the following categories: “Large” for priority nucleus with area coverage
1301 equal to or larger than 1,000 km²; “Medium” for priority nucleus with area coverage equal
1302 to or larger than 250 km² and smaller than 1,000 km²; and “Small” for priority nucleus
1303 with area coverage smaller than 250 km². We consider that continuous areas of more than
1304 1,000 km² represent enough available habitat for maintaining a viable population of most
1305 of the included species.

1306 3.3 Results

1307 Of the 337 analyzed species, 262 (77.4%) have been assessed by IUCN. Of those, 39
1308 (11.5%) are considered threatened, including 17 Vulnerable, 15 Endangered, and seven
1309 Critically Endangered ([Appendix S2](#)). Sixty-one species are considered Data Deficient,
1310 of which 57 (93.4%) were described more than 10 years ago. Amongst the 75 species not
1311 assessed by IUCN, 77% (N = 58) are restricted-range species, and the remaining 23% (N
1312 = 17) are partially-distributed species.

1313 The current PA network covers 10.25% of the Cerrado and putatively protects on
1314 average 21.47% of the distributions of endemic terrestrial vertebrates. Four species are
1315 completely absent from the system ([Appendix S3](#)). According to the prioritization, using

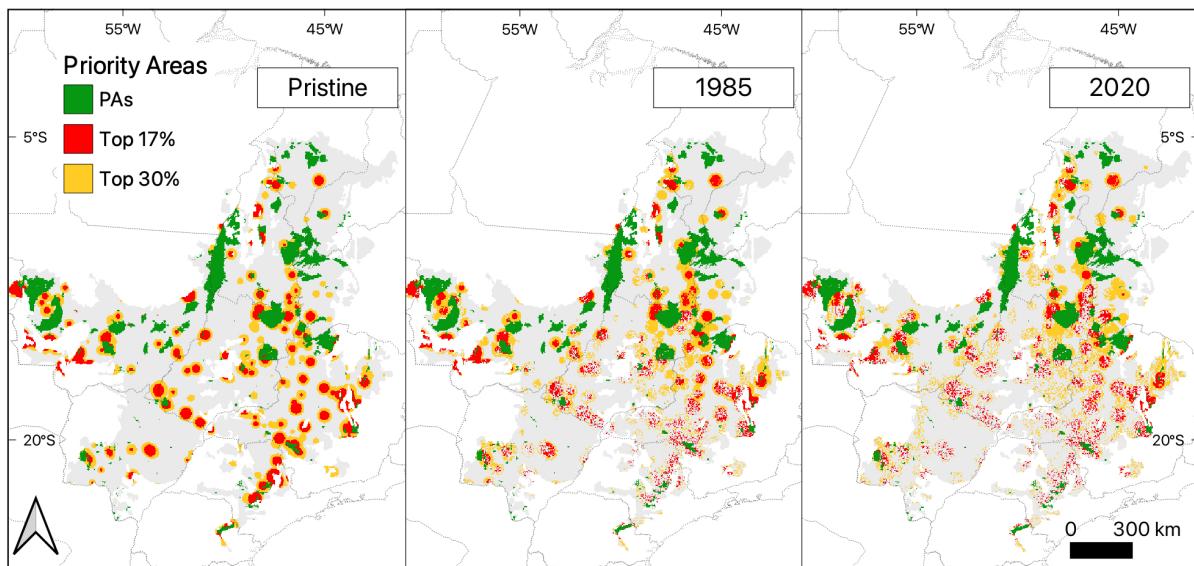


Figure 9 – Priority areas for the conservation of Cerrado endemic terrestrial vertebrate species, in three distinct land-use scenarios (Pristine, 1985 and 2020) and two conservation targets (top 17% and 30% of the ecoregion).

the most recent land-use map (2020 scenario), protecting an additional 6.75% of the region (~135,000 km², i.e. 17% of the Cerrado) would represent at least 10% of each distribution and increase the average representation to 43.5%. In comparison, the protection of 30% of top priority areas would increase this figure by an additional 12.7%, representing at least 16.6% of each distribution and an average of 56.2% of mapped ranges. Detailed information on species representation in the current PA network and in each conservation target can be found in the supplementary material ([Appendix S3](#)).

Despite the similar overall location of the top 17% and 30% priority areas, in the pristine scenario the priority areas were represented only by patches of continuous land, while in the 1985 and 2020 scenarios top priority areas also comprise some sparsely distributed discontinuous areas ([Figure 9](#)). While in the pristine scenario continuous priority areas were spread across the Cerrado, in the 1985 and 2020 scenarios they were concentrated in the northern portion of the region, while largely segregated priority areas were mostly spread over the southern portion ([Figure 9](#)). As for the patch size analysis of the top 17% priority areas, opportunities to create, expand and connect PAs in large continuous extensions of natural habitats were concentrated in Mato Grosso, Minas Gerais, Goiás and Tocantins states ([Figure 10; Box 1](#)). On the other hand, patches of medium to small priority areas are scattered throughout the southern portion of the region ([Figure 10](#)).

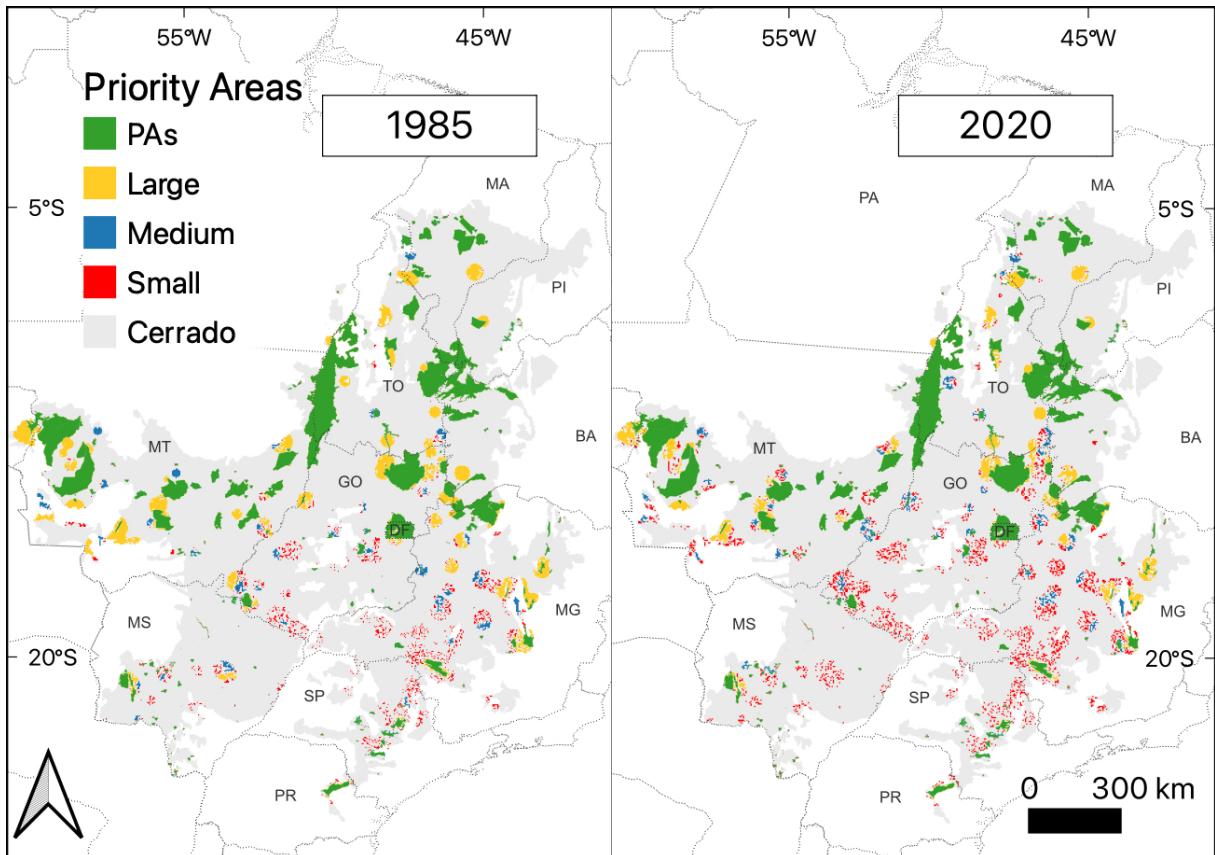


Figure 10 – Top 17% of the Cerrado ecoregion for the conservation of endemic terrestrial vertebrate species, classified into three categories according to the territorial extension achieved upon the creation of protected areas. Thresholds considered were: over 1000 km² for “Large” areas, and under 250 km² for “Small” ones. Areas between 250 km² and 1000 km² were considered as “Medium”. State initials stand for: BA: Bahia; DF: Distrito Federal; GO: Goiás; MA: Maranhão; MG: Minas Gerais; MS: Mato Grosso do Sul; MT: Mato Grosso; PA: Pará; PI: Piauí; PR: Paraná; SP: São Paulo and TO: Tocantins.

1334

Box 1: In Mato Grosso, priorities are to the northward expansion of the Chapada dos

Guimarães National Park preferably aiming for the connection to the APA Cabeceiras do Rio Cuiabá. Our results also highlight the need to expand the Serra das Araras Ecological Station, and to implement new protected areas on the border and across the eastern portion of the Rondônia state coupled with the aim of connecting large extensions of indigenous lands in the westernmost limits of the Cerrado ([Figure 10](#)). In Minas Gerais state, the focus should be given to the expansion and connection of the Sempre Vivas National Park with Rio Preto and Biribiri State Parks, as well as for the connection between the Grão Mogol and Botumirim State Parks with the Acauã Ecological Station. Our results also highlight an opportunity for great expansion around the Serra do Cabral State Park, a moderate expansion around the Serra da Canastra National Park, and the opportunity to create a large protected area in northwestern Minas Gerais, near the small Sagarana State Park ([Figure 10](#)). In the northeastern portion of the Goiás state, at the border with Bahia, there is an opportunity to expand and connect the protected areas located at the Serra Geral plateau. As for northern Goiás and southern Tocantins, large extensions of natural habitat can be protected by the expansion of the Chapada dos Veadeiros National Park, and the APA Minaçu, aiming for connections with APA Pouso Alto in the east, and with APA Lago de São Salvador do Tocantins, Paranã and Palmeirópolis in the north ([Figure 10](#)). Finally, for the northern portion of the Tocantins state our results highlight the opportunity to expand the APA Serra do Lageado; to expand the Árvores Fossilizadas Natural Monument aiding in the connection with the Chapada das Mesas National Park in eastern Maranhão state, and for the creation of a new protected area on the upper Tocantins river valley at the municipality of Guaraí. Notwithstanding, a large priority area is located in the municipality of Loreto in eastern Maranhão state, and an eastward expansion of Urucuí-Una Ecological Station in Piauí state is also amongst the top 17% large priority areas ([Figure 10](#)).

1335

1336 The analyses of priority areas considering temporal series of LULC changes revealed
1337 a clear negative effect of postponing conservation action in the Cerrado. Opportunities
1338 to represent endemic terrestrial vertebrate distributions decreased with the conversion of
1339 natural habitats into anthropic uses ([Table 5](#), [Figure 11](#)). The average species distribution
1340 representation in large areas decreased as we compare the prioritization outcomes of recent
1341 land-use changes (from 17.3% to 12.2% in the 1985 and 2020 scenarios respectively, a
1342 difference of $\sim -5.1\%$). On the contrary, the representation of species distributions in
1343 combined small and medium fragmented priority areas increased over time (from 7.4% to
1344 10.2% in the 1985 and 2020 scenarios respectively, a difference of $\sim +2.8\%$; [Figure 11](#)).

Table 5 – Percentage of endemic terrestrial vertebrate distribution representation in priority areas according to two targets of land protection in different scenarios of past land-use in the Brazilian Cerrado.

	Representantion	
	Top 17%	Top30%
Pristine	48.60%	73.66%
1985	45.58%	63.46%
1990	45.01%	61.34%
1995	44.49%	59.97%
2000	44.10%	58.78%
2005	43.95%	57.87%
2010	43.75%	57.21%
2015	43.82%	56.90%
2020	43.30%	55.84%

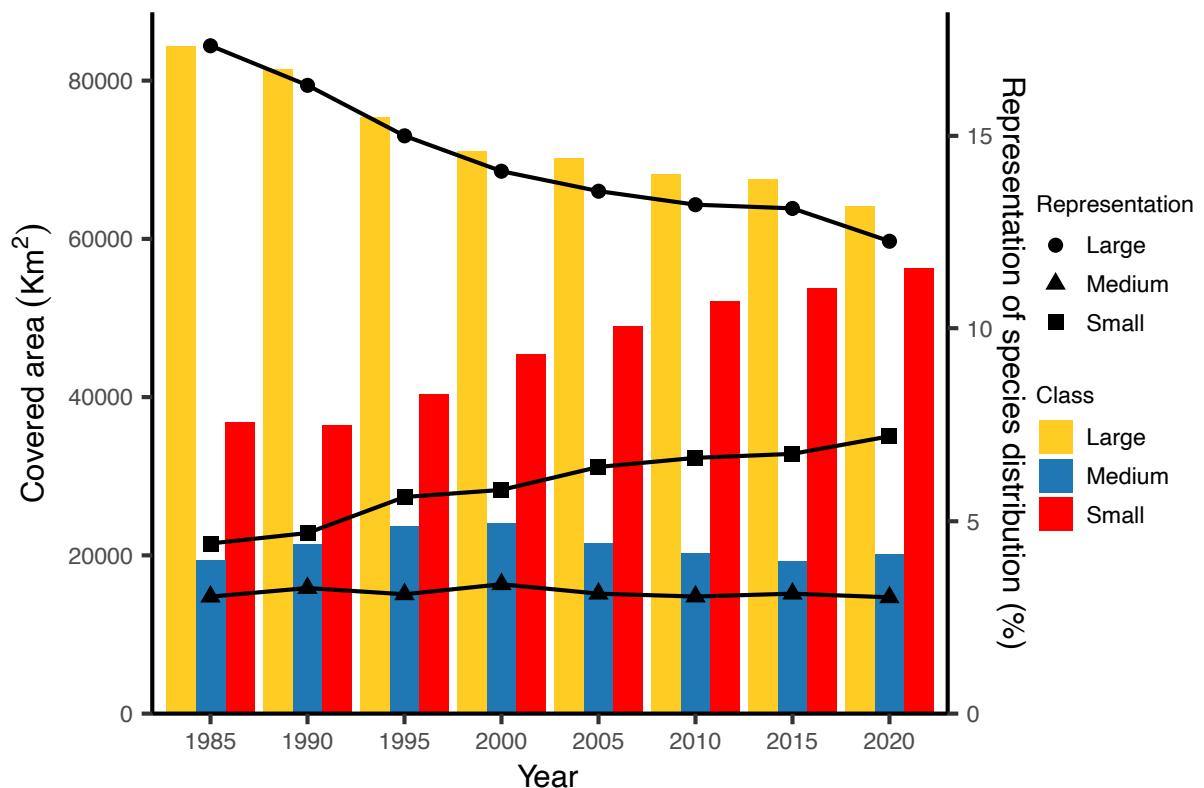


Figure 11 – Changes in the total area covered by three different size categories of the top 17% priority areas for the conservation of Cerrado endemic terrestrial vertebrate species throughout time and respective percentage of species distributions within each category. Thresholds considered were: over 1000 km² for “Large” areas, and under 250 km² for “Small” ones. Areas between 250 km² and 1000 km² were considered as “Medium”.

1345 3.4 Discussion

1346 In agreement with previous studies (e.g. Prieto-Torres et al., 2022; Prieto-Torres,
1347 Lira-Noriega, & Navarro-Sigüenza, 2020), our findings suggest a suboptimal distribution
1348 of current Cerrado PAs. Considering that this region was pointed long ago as a biodiversity
1349 hotspot (Myers et al., 2000) and is currently a deforestation frontier (P. Pacheco et al.,
1350 2021), strategic land-use planning is a pending issue that should be urgently addressed
1351 (Lemes et al., 2020; Strassburg et al., 2017). Otherwise, conservation opportunities will
1352 continue diminishing with the increase in habitat loss and fragmentation in these highly
1353 diverse savannas (Nori et al., 2013; Resende, Cimon-Morin, Poulin, Meyer, & Loyola,
1354 2019).

1355 Herein we identified strategic areas to efficiently expand the Cerrado PA network.
1356 Most importantly, relatively small increments in the total protected area resulted in a
1357 significant increase in species representation. The 17% land protection target was due in
1358 2020 (CBD, 2010) and has not been achieved yet, therefore the protection of the Brazilian
1359 Cerrado lags far behind the new ambitious target (30%; Woodley et al., 2019). By com-
1360 paring priority areas across different periods during the last decades, we pinpointed that
1361 habitat loss and fragmentation are the most important factors behind the rapid loss of
1362 conservation opportunities in the Cerrado (see also Grande et al., 2020). While opportu-
1363 nities to increase the representation of species distributions did not decrease sharply over
1364 time, the top priority areas became smaller and fragmented as time passed. As a con-
1365 sequence, opportunities to represent species distributions in large priority areas (>1000
1366 km^2) are decreasing as a result of the conversion of natural habitats into anthropic land
1367 use. Noteworthy, the increase in small and medium priority areas does not surpass the
1368 decrease of representation in larger ones, suggesting that the protection of large priority
1369 areas in the Cerrado should be more urgent than the protection of the smallest areas that
1370 have remained after the northward shift in the deforestation frontier (Betts et al., 2017;
1371 De Marco Jr. et al., 2020).

1372 Habitat connectivity in the Cerrado has decreased sharply during the last decades,
1373 mostly due to the loss of connecting fragments. Unfortunately, connectivity is being
1374 lost faster than the loss of natural habitats and we are close to a lower threshold of
1375 remaining habitats below which connectivity becomes severely compromised (Grande et
1376 al., 2020). Considering the habitat requirements of many of the species assessed here, large
1377 portions of connected natural environments are important to safeguard the maintenance
1378 of ecological processes (Betts et al., 2017; Díaz et al., 2018). The northern portion of
1379 the region encompasses the largest continuous priority areas even in the most recent and
1380 pessimistic land-use scenario. Worryingly, the Deforestation Front report (P. Pacheco et
1381 al., 2021) highlights the northern portion of the Cerrado as the most impacted worldwide
1382 and forecasts a trend of persistent deforestation in the region. This evidence, coupled with
1383 our results, suggests a clear trend of further reduction of conservation opportunities if no

1384 actions are urgently taken to halt habitat loss in the Cerrado, especially in its northern
1385 portion (Nori et al., 2013; Resende et al., 2019). Although the small and isolated priority
1386 areas detected here might not be adequate for some of our target species (see De Marco Jr.
1387 et al., 2020), those located in the southern portion of the Cerrado are the last remaining
1388 habitat for many endemic vertebrate species studied herein and must not be overlooked.

1389 Some regions of the northern portion of the Cerrado (e.g. Serra Geral plateau)
1390 remained climatically stable during the Quaternary climatic fluctuations (Werneck et al.,
1391 2012). This climatic stability conferred a conservation uniqueness in light of global climate
1392 change. Moreover, a study using a framework directed to halt vegetation loss combined
1393 with predictions of species distributions under climate change scenarios highlights priority
1394 areas for plant conservation in northern Cerrado (Monteiro et al., 2020), converging with
1395 our proposal, and others (e.g. Brum, Pressey, Bini, & Loyola, 2019; Diniz-Filho et al.,
1396 2020; P. Pacheco et al., 2021). For future scenarios, however, the southern portion of the
1397 Cerrado is hypothesized to be climatically stable (De Marco Jr. et al., 2020; Diniz-Filho
1398 et al., 2020). So, the last remnants in the highly impacted southern portions should be
1399 preserved and reconnected via restoration activities (Strassburg et al., 2017). There is an
1400 opportunity to safeguard enough protection for species while also increasing agricultural
1401 production without impacting the remaining natural habitats in the Cerrado (Strassburg
1402 et al., 2017). This “greener scenario” and zero deforestation approach points also to the
1403 necessity of implementing restoration in critical areas, mostly in the southern portion of
1404 the ecoregion. In this sense, following our prioritization scheme and considering both
1405 the threat of current deforestation in northern Cerrado and the outstanding presence of
1406 discontinuous priority areas in the southern portion of the region (Grande et al., 2020), we
1407 propose the urgent implementation of new PAs on the northern Cerrado as the last chance
1408 to maintain naturally connected areas. In addition, the focus on restoration approaches
1409 should be directed towards the southern priority areas, especially those with the potential
1410 to be connected to compose conservation mosaics.

1411 In fact, small and fragmented areas in southern Cerrado may serve as the backbone
1412 of larger conservation strategies focused on landscape connectivity and widespread, thre-
1413 atened species. Moreover, as most of our target species are relatively small-ranged and
1414 regionalized (Azevedo et al., 2016; Nogueira et al., 2011), given that creating large and
1415 continuous PAs is not a possibility, the question of conserving southern Cerrado endemics,
1416 is more of a problem of correctly locating PAs. Although small and highly fragmented,
1417 the few remaining Cerrado areas in the south are still home to hundreds of endemic ver-
1418 tebrate species studied herein. To lose more habitat in these areas would lead to very
1419 high extinction rates in the Cerrado, which would not be compensated by actions in the
1420 more connected and extensive northern areas. In agreement with previous biogeographical
1421 studies in the Cerrado, detecting complex, regionalized, and significantly co-distributed
1422 allopatric biotas (Azevedo et al., 2016; Nogueira et al., 2011), our priority areas span

1423 different portions of the Cerrado. Thus, resulting conservation strategies must adapt to
1424 each subregional land use context. In this sense, it is imperative to halt deforestation in
1425 the entire Cerrado, both in the highly fragmented south and in the current deforestation
1426 frontier in the north. Additionally, it would be essential to guarantee the representation
1427 of most of the Cerrado vegetational gradient as possible, since not only vascular plants
1428 (see Durigan, Siqueira, Franco, Bridgewater, & Ratter, 2003), but all endemic terrestrial
1429 vertebrate groups analyzed here (e.g. Carmignotto et al., 2022; Nogueira et al., 2011;
1430 Valdujo et al., 2012) include habitat specialists depending on different habitats covering
1431 the Cerrado ecoregion, from gallery forest to savannas, woodlands, wetlands, and open
1432 grasslands.

1433 The number of Data Deficient species and those not yet assessed by IUCN highlights
1434 a major knowledge shortfall that might hamper accurate policy-making in Cerrado. This
1435 implies that research investment aimed to fill knowledge gaps on these species could be
1436 considered a strategic investment to reach accurate conservation recommendations (Nori,
1437 Loyola, & Villalobos, 2020; Nori et al., 2018). Noteworthy more than half of the Cerrado
1438 endemic terrestrial vertebrate species classified as DD are amphibians (Appendix S3). It
1439 has been shown that most DD amphibians are facing a high extinction risk, especially in
1440 Brazil (Morais et al., 2013). Efforts to reduce the proportion of DD species on the IUCN
1441 redlist should be mandatory as this general “non-threatened” category is often overlooked
1442 by both the scientific community and decision-makers, leading to biased conservation
1443 recommendations (Nori et al., 2018).

1444 Recent studies focused on the conservation of ecosystem services also highlight that
1445 time is critical for conserving the Brazilian Cerrado (Resende et al., 2019). Projections of
1446 land-use conversion under a business-as-usual scenario and forecasted extinctions in the
1447 next 30 years are clear proof that not only conservation policies should be immediately
1448 directed towards the protection of the Brazilian Cerrado, but also the whole coopera-
1449 tion of public and private sectors is necessary to achieve meaningful conservation results
1450 (Strassburg et al., 2017). If policy-making is not urgently focused on protecting strategic
1451 remnants of the Cerrado hotspot, halting habitat fragmentation, and using habitat res-
1452 toration as a key activity (see Strassburg et al., 2017), the future of the diverse endemic
1453 fauna of the central Brazilian savannas is clearly somber. However, the only way to achi-
1454 eve it will be through a joint effort of researchers, policy-makers, NGOs, and the private
1455 sector. In the era of delivery, not promises (Loyola, 2022), “tomorrow” might be too late.

1456 3.5 Supporting information

1457 Disclaimer

1458 A numeração dos apêndices 2 e 3 estão diferentes da do artigo original ([Vieira-](#)
 1459 [Alencar et al., 2023](#)) em razão da inclusão do texto completo dos materiais e métodos
 1460 (originalmente Appendix S2) diretamente na tese.

1461 Appendix S1

1462 MapBiomas land-use and land-cover (LULC) classification and respective binary reclas-
 1463 sification codes. Data were obtained and processed on Google Earth Engine, and the
 1464 complete reclassification algorithm is available [here](#)

Natural/Anthropic	Nomenclature	MapBiomas ID	Reclass Code
Mosaic	1. Forest	1	0
Natural	1.1. Natural Forest	3	0
Natural	1.2. Savanna Formation	4	0
Natural	1.3. Mangrove	5	0
Natural	1.4. Wooded Restinga	49	0
Mosaic	2. Non Forest Natural Formation	10	0
Natural	2.1. Wetland	11	0
Natural	2.2. Grassland	12	0
Natural	2.3. Salt Flat	32	0
Natural	2.4. Rocky Outcrop	29	0
Natural	2.5. Other non Forest Formations	13	0
Mosaic	3. Farming	14	1
Anthropic	3.1. Pasture	15	1
Anthropic	3.2. Agriculture	18	1
Anthropic	3.2.1. Temporary Crop	19	1
Anthropic	3.2.1.1. Soybean	39	1
Anthropic	3.2.1.2. Sugar Cane	20	1
Anthropic	3.2.1.3. Rice	40	1
Anthropic	3.2.1.4. Other Temporary Crops	41	1
Anthropic	3.2.2. Perennial Crop	36	1
Anthropic	3.2.2.1. Coffee	46	1
Anthropic	3.2.2.2. Citrus	47	1
Anthropic	3.2.2.3. Other Perennial Crop	48	1
Anthropic	3.3. Forest Plantation	9	1
Anthropic	3.4 Mosaic Agriculture and Pasture	21	1
Mosaic	4. Non-vegetated Area	22	1
Natural	4.1. Beach, Dune and Sand Spot	23	0
Anthropic	4.2. Urban Area	24	1
Anthropic	4.3. Mining	30	1
Mosaic	4.4. Other non Vegetated Areas	25	1
Mosaic	5. Water	26	1
Mosaic	5.1. River, Lake and Ocean	33	1
Anthropic	5.2. Aquaculture	31	1
Non Identified	6. Non-Observed	27	1

1465 Appendix S2

1466 Number of species of each terrestrial vertebrate group in each IUCN threat category. N =
 1467 Absolute number; WG = percentages of each IUCN threat category within each terrestrial
 1468 vertebrate group (column sum = 1); WC = percentages of each terrestrial vertebrate
 1469 group within each IUCN threat category (WCs in one line sum = 1). Categories based on
 1470 ([IUCN, 2022](#)) are: LC = Least Concern; NT = Near Threatened; VU = Vulnerables; EN
 1471 = Endangered; CR = Critically Endangered; DD = Data-Deficient; NA = Non-Assessed

Categories	Amphibians			Lizards			Snakes			Birds			Mammals		
	N	WG	WC	N	WG	WC	N	WG	WC	N	WG	WC	N	WG	WC
LC	41	0.33	0.28	34	0.52	0.23	36	0.56	0.24	20	0.45	0.14	16	0.41	0.11
NT	2	0.02	0.13	2	0.03	0.13	1	0.02	0.07	8	0.18	0.54	2	0.05	0.13
VU	0	0	0	2	0.03	0.12	5	0.08	0.29	9	0.2	0.53	1	0.03	0.06
EN	0	0	0	3	0.05	0.2	2	0.03	0.14	5	0.11	0.33	5	0.13	0.33
CR	3	0.02	0.43	2	0.03	0.29	1	0.02	0.14	1	0.02	0.14	0	0	0
DD	36	0.29	0.57	10	0.15	0.16	8	0.13	0.13	0	0	0	7	0.18	0.14
NA	42	0.34	0.56	13	0.2	0.17	10	0.16	0.13	2	0.04	0.03	8	0.2	0.11

1472 Appendix S3

1473 Cerrado endemic terrestrial vertebrate species distribution representation in three distinct
 1474 land protection thresholds. The proportion represented under each threshold considers
 1475 the most recent land-use scenario available in [MapBiomas \(2022\)](#). PAs: Representation
 1476 under current Cerrado's protected area network; Top 17%: Representation under the
 1477 protection of the top 17% of the land in the Cerrado; Top 30%: Representation under the
 1478 protection of the top 30% of the land in the Cerrado.

	PAs	Top 17%	Top 30%
Average representation	21.47	43.56	56.18
<i>Adenomera cotuba</i>	15.90	28.40	59.30
<i>Adenomera saci</i>	26.30	43.00	57.20
<i>Akodon kadiweu</i>	45.70	67.90	77.50
<i>Akodon lindberghi</i>	44.40	57.00	62.60
<i>Alectrurus tricolor</i>	22.90	32.10	41.60
<i>Alipiopsitta xanthops</i>	12.40	22.70	38.60
<i>Allobates brunneus</i>	21.50	55.30	74.20
<i>Allobates goianus</i>	28.00	51.50	67.60
<i>Alopoglossus collii</i>	19.70	69.50	71.50
<i>Ameerega berothoka</i>	2.10	18.00	31.00
<i>Ameerega braccata</i>	57.70	77.30	84.00
<i>Ameerega flavopicta</i>	21.80	38.00	56.40
<i>Ameerega picta</i>	18.80	41.50	57.80

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	PAs	Top 17%	Top 30%
<i>Ameiva jacuba</i>	28.50	41.10	48.60
<i>Ameiva parecis</i>	4.00	77.60	80.70
<i>Ameivula cipoensis</i>	39.80	70.50	71.00
<i>Ameivula jalapensis</i>	37.10	59.40	94.30
<i>Ameivula mumbuca</i>	37.80	50.30	95.00
<i>Ameivula xacriaba</i>	21.40	33.00	78.60
<i>Amphisbaena absaberi</i>	5.50	66.00	66.50
<i>Amphisbaena acrobeles</i>	92.80	98.80	100.00
<i>Amphisbaena anaemariae</i>	26.20	34.40	44.20
<i>Amphisbaena bedai</i>	3.40	19.80	31.20
<i>Amphisbaena brevis</i>	15.20	67.50	74.30
<i>Amphisbaena carli</i>	14.30	36.90	67.20
<i>Amphisbaena crisae</i>	50.80	62.50	73.20
<i>Amphisbaena cuiabana</i>	32.40	43.90	61.90
<i>Amphisbaena filiformis</i>	3.70	42.60	77.20
<i>Amphisbaena kraoh</i>	50.50	61.60	78.60
<i>Amphisbaena leeseri</i>	1.70	14.60	27.60
<i>Amphisbaena maranhensis</i>	0.70	63.80	93.10
<i>Amphisbaena mebengokre</i>	0.00	24.90	26.80
<i>Amphisbaena neglecta</i>	67.10	81.80	86.70
<i>Amphisbaena persephone</i>	3.40	56.00	64.80
<i>Amphisbaena sanctaeritae</i>	8.20	21.80	21.90
<i>Amphisbaena saxosa</i>	55.40	86.90	88.80
<i>Amphisbaena silvestrii</i>	20.30	35.50	51.70
<i>Amphisbaena steindachneri</i>	7.70	65.20	65.90
<i>Amphisbaena talisiae</i>	38.10	52.30	65.00
<i>Anolis meridionalis</i>	20.60	39.80	53.40
<i>Antilophia galeata</i>	15.20	28.50	41.70
<i>Aplastodiscus lutzorum</i>	37.40	45.30	60.60
<i>Apostolepis adhara</i>	10.60	59.70	86.90
<i>Apostolepis albicollaris</i>	22.60	39.20	51.00
<i>Apostolepis assimilis</i>	10.30	21.70	29.70
<i>Apostolepis barrioi</i>	3.10	14.30	20.50
<i>Apostolepis cerradoensis</i>	27.70	78.30	83.20
<i>Apostolepis christineae</i>	10.90	77.30	80.20
<i>Apostolepis flavotorquata</i>	28.20	43.80	52.70

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	PAs	Top 17%	Top 30%
<i>Apostolepis goiasensis</i>	18.70	35.00	42.20
<i>Apostolepis intermedia</i>	16.40	28.30	43.50
<i>Apostolepis kikoi</i>	8.00	55.00	61.50
<i>Apostolepis lineata</i>	67.10	81.80	86.70
<i>Apostolepis longicaudata</i>	39.30	49.40	78.60
<i>Apostolepis nelsonjorgei</i>	59.00	75.90	85.40
<i>Apostolepis phillipsae</i>	14.90	55.00	55.00
<i>Apostolepis polylepis</i>	31.30	46.30	71.30
<i>Apostolepis sanctaeritae</i>	22.40	35.60	53.10
<i>Apostolepis serrana</i>	7.00	54.90	57.20
<i>Apostolepis striata</i>	21.70	72.10	73.10
<i>Apostolepis tertulianobeui</i>	26.30	52.00	63.20
<i>Apostolepis vittata</i>	31.30	69.20	74.90
<i>Arremon flavirostris</i>	8.40	19.80	30.80
<i>Asthenes luizae</i>	32.20	65.70	70.90
<i>Atractus albuquerquei</i>	14.40	36.90	45.50
<i>Atractus edioi</i>	18.20	76.30	86.70
<i>Atractus pantostictus</i>	16.80	35.60	48.70
<i>Atractus spinalis</i>	52.00	78.30	78.40
<i>Atractus stygius</i>	3.50	39.60	64.70
<i>Augastes scutatus</i>	20.20	54.50	65.90
<i>Bachia bresslaui</i>	34.40	47.20	57.70
<i>Bachia cacerensis</i>	11.20	57.80	58.20
<i>Bachia didactyla</i>	23.50	52.10	59.20
<i>Bachia geralista</i>	23.70	41.80	73.80
<i>Bachia micromela</i>	0.00	74.20	79.50
<i>Bachia oxyrhina</i>	67.50	67.80	92.60
<i>Bachia psamophila</i>	38.60	82.60	83.50
<i>Barycholos ternetzi</i>	12.90	31.20	52.60
<i>Boana botumirim</i>	11.20	66.90	87.70
<i>Boana buriti</i>	18.60	37.50	54.00
<i>Boana caiapo</i>	17.10	27.50	41.40
<i>Boana cipoensis</i>	18.80	53.70	70.60
<i>Boana ericae</i>	82.90	86.20	95.70
<i>Boana goiana</i>	33.90	41.90	61.50
<i>Boana jaguariaicensis</i>	47.20	61.40	63.90

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	PAs	Top 17%	Top 30%
<i>Boana lundii</i>	14.80	30.60	45.40
<i>Boana stenocephala</i>	1.60	25.70	26.10
<i>Bokermannohyla alvarengai</i>	22.50	57.90	71.30
<i>Bokermannohyla ibitiguara</i>	30.20	49.40	50.40
<i>Bokermannohyla izecksohni</i>	15.70	29.80	29.80
<i>Bokermannohyla nanuzae</i>	19.60	68.60	71.70
<i>Bokermannohyla napolii</i>	1.40	25.90	29.00
<i>Bokermannohyla pseudopseudis</i>	47.30	57.50	76.50
<i>Bokermannohyla raviga</i>	3.90	33.00	34.60
<i>Bokermannohyla sagarana</i>	4.60	55.40	58.40
<i>Bokermannohyla sapiranga</i>	27.60	38.60	54.90
<i>Bokermannohyla saxicola</i>	18.50	53.10	67.70
<i>Bokermannohyla sazimai</i>	8.20	28.10	32.30
<i>Bothrops itapetiningae</i>	10.70	19.50	25.90
<i>Bothrops marmoratus</i>	19.20	33.70	52.70
<i>Bothrops moojeni</i>	8.50	19.00	30.10
<i>Bothrops pauloensis</i>	7.80	18.30	24.90
<i>Calassomys apicalis</i>	9.40	62.20	69.90
<i>Callithrix penicillata</i>	18.80	31.30	42.50
<i>Calomys tocantinsi</i>	34.20	46.50	63.60
<i>Carterodon sulcidens</i>	27.00	52.50	62.40
<i>Celeus obrieni</i>	8.80	18.80	42.80
<i>Cercomacra ferdinandi</i>	26.50	40.90	69.20
<i>Cerradomys akroai</i>	14.70	52.20	87.50
<i>Cerradomys marinhus</i>	10.90	26.60	45.10
<i>Cerradomys scotti</i>	21.40	35.80	50.60
<i>Charitospiza eucosma</i>	15.80	27.80	44.00
<i>Chiasmocleis albopunctata</i>	14.10	35.90	52.80
<i>Chiasmocleis centralis</i>	4.60	37.40	41.50
<i>Chironius brazili</i>	20.20	38.20	49.10
<i>Cinclodes espinhacensis</i>	39.20	67.60	69.20
<i>Clibanornis rectirostris</i>	7.70	18.80	31.60
<i>Clyomys laticeps</i>	24.60	39.50	46.30
<i>Coleodactylus brachystoma</i>	18.50	40.00	65.00
<i>Colobosaura modesta</i>	21.90	40.80	57.10
<i>Columbina cyanopis</i>	10.20	41.10	53.50

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Appendix S3 – Continued from previous page

	PAs	Top 17%	Top 30%
<i>Conothraupis mesoleuca</i>	15.20	34.70	51.10
<i>Coryphaspiza melanotis</i>	13.40	25.80	38.20
<i>Crossodactylus franciscanus</i>	22.40	40.80	42.10
<i>Crossodactylus trachystomus</i>	17.70	58.70	66.10
<i>Ctenomys bicolor</i>	4.60	32.80	54.00
<i>Ctenomys nattereri</i>	9.90	49.00	64.10
<i>Cyanocorax cristatellus</i>	10.80	22.00	34.50
<i>Dendropsophus anataliasiasi</i>	12.30	26.60	46.10
<i>Dendropsophus araguaya</i>	2.10	35.20	40.00
<i>Dendropsophus cerradensis</i>	2.50	19.70	20.20
<i>Dendropsophus cruzi</i>	10.30	29.90	48.90
<i>Dendropsophus elianeae</i>	8.60	22.00	31.30
<i>Dendropsophus jimi</i>	9.90	22.30	31.00
<i>Dendropsophus rhea</i>	9.10	20.60	20.70
<i>Dendropsophus rubicundulus</i>	11.90	27.50	51.40
<i>Dendropsophus tritaeniatus</i>	17.80	32.70	50.30
<i>Drymoluber brasili</i>	10.50	23.00	31.50
<i>Elachistocleis bumbameuboi</i>	13.30	76.40	93.40
<i>Elachistocleis matogrossos</i>	12.50	25.70	51.70
<i>Embernagra longicauda</i>	12.60	40.90	60.80
<i>Enyalius capetinga</i>	36.40	43.90	67.30
<i>Epicrates crassus</i>	12.00	23.70	36.50
<i>Epictia clinorostris</i>	6.70	28.60	42.10
<i>Erythrolamprus maryellenae</i>	40.90	55.00	66.20
<i>Eurolophosaurus nanuzae</i>	25.90	68.20	70.90
<i>Euryoryzomys lamia</i>	23.70	37.80	57.10
<i>Euscarthmus rufomarginatus</i>	19.60	29.20	51.10
<i>Galea flavidens</i>	26.00	40.80	55.60
<i>Geositta poeciloptera</i>	23.70	34.10	46.30
<i>Guaramemua affine</i>	27.80	37.80	54.20
<i>Gyldenstolpia planaltensis</i>	58.80	71.20	77.60
<i>Gymnodactylus amarali</i>	19.00	36.30	61.20
<i>Gymnodactylus guttulatus</i>	15.50	87.00	88.30
<i>Helicops boitata</i>	6.50	43.40	44.80
<i>Helicops gomesi</i>	7.00	12.10	18.40
<i>Helicops phantasma</i>	24.90	47.30	71.50

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Appendix S3 – Continued from previous page

	PAs	Top 17%	Top 30%
<i>Herpsilochmus longirostris</i>	6.90	15.60	26.50
<i>Heterodactylus lundii</i>	25.20	54.00	56.40
<i>Holochilus sciureus</i>	14.70	33.40	52.10
<i>Hoplocercus spinosus</i>	19.90	36.10	48.40
<i>Hydropsalis candidans</i>	9.20	22.20	32.70
<i>Hylodes otavioi</i>	36.50	68.20	68.50
<i>Ischnocnema penaxavantinho</i>	0.80	25.10	31.80
<i>Kentropyx paulensis</i>	25.30	38.20	48.30
<i>Kentropyx vanzoi</i>	18.50	48.70	59.40
<i>Kerodon acrobata</i>	8.80	40.30	59.00
<i>Knipolegus franciscanus</i>	12.60	26.60	48.70
<i>Kunsia tomentosus</i>	24.30	60.60	62.70
<i>Laterallus xenopterus</i>	11.10	19.40	35.80
<i>Leposternon cerradensis</i>	3.10	19.80	20.00
<i>Leposternon maximus</i>	38.70	48.30	75.30
<i>Leposternon mineiro</i>	0.00	30.30	41.60
<i>Leptodactylus brevipes</i>	15.90	29.60	52.90
<i>Leptodactylus camaquara</i>	22.70	59.20	78.20
<i>Leptodactylus cunicularius</i>	27.20	67.30	68.80
<i>Leptodactylus furnarius</i>	17.40	39.50	48.40
<i>Leptodactylus kilombo</i>	0.80	31.40	48.70
<i>Leptodactylus pustulatus</i>	8.80	26.50	48.20
<i>Leptodactylus sertanejo</i>	28.10	44.40	59.90
<i>Leptodactylus tapiti</i>	84.20	87.50	93.80
<i>Liopholops schubarti</i>	3.80	23.70	24.20
<i>Liopholops taylori</i>	10.90	77.30	80.20
<i>Lonchophylla bokermanni</i>	43.20	81.50	81.80
<i>Lonchophylla dekeyseri</i>	38.30	47.50	61.40
<i>Lycalopex vetulus</i>	18.20	32.40	45.00
<i>Lygophis paucidens</i>	36.10	49.30	67.80
<i>Lysapsus caraya</i>	29.80	39.90	57.10
<i>Manciola guaporicola</i>	32.10	50.80	61.20
<i>Melanopareia torquata</i>	19.40	33.40	47.20
<i>Micrablepharus atticolus</i>	19.40	38.30	51.20
<i>Microakodontomys transitorius</i>	59.70	68.30	73.60
<i>Microspingus cinereus</i>	17.20	35.20	50.20

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Appendix S3 – Continued from previous page

	PAs	Top 17%	Top 30%
<i>Micrurus brasiliensis</i>	32.70	48.50	68.50
<i>Micrurus tricolor</i>	7.80	18.00	39.30
<i>Monodelphis kunsi</i>	15.40	34.50	48.50
<i>Monodelphis sanctaerosae</i>	10.40	61.30	68.20
<i>Myiothlypis leucophrys</i>	17.60	27.70	39.40
<i>Neothraupis fasciata</i>	18.40	31.00	46.60
<i>Nothura minor</i>	22.20	33.90	41.00
<i>Nyctiprogne vielliardi</i>	5.90	30.50	45.20
<i>Nystalus striatipectus</i>	3.10	11.40	27.80
<i>Odontophrynus cultripes</i>	13.60	28.60	40.10
<i>Odontophrynus juquinha</i>	17.00	57.80	68.40
<i>Odontophrynus monachus</i>	31.80	50.90	51.60
<i>Oecomys cleberi</i>	15.50	26.20	36.90
<i>Oligoryzomys moojeni</i>	25.50	42.90	72.80
<i>Oligoryzomys rupestris</i>	79.90	91.10	91.40
<i>Oreobates antrum</i>	18.70	40.70	53.60
<i>Oreobates heterodactylus</i>	24.80	52.50	73.70
<i>Oreobates remotus</i>	50.60	78.80	88.00
<i>Oxymycterus delator</i>	39.20	51.10	63.40
<i>Oxymycterus itapeby</i>	46.60	60.60	63.20
<i>Paroaria baeri</i>	25.70	33.70	48.30
<i>Penelope ochrogaster</i>	14.70	28.90	50.30
<i>Phaethornis nattereri</i>	12.80	26.40	42.20
<i>Phalotris cerradensis</i>	37.90	64.70	87.30
<i>Phalotris concolor</i>	1.80	39.50	56.20
<i>Phalotris labiomaculatus</i>	25.60	52.10	83.20
<i>Phalotris lativittatus</i>	5.70	16.90	21.00
<i>Phalotris matogrossensis</i>	4.90	18.20	29.50
<i>Phalotris mertensi</i>	5.80	13.60	18.80
<i>Phalotris multipunctatus</i>	13.60	28.20	28.80
<i>Phalotris nasutus</i>	14.00	24.80	33.70
<i>Phasmahyla jandaia</i>	19.00	53.00	66.20
<i>Philodryas livida</i>	16.70	30.40	35.70
<i>Philodryas mattogrossensis</i>	2.40	14.90	22.60
<i>Phyllomyias reiseri</i>	16.00	30.00	49.70
<i>Phyllomys brasiliensis</i>	6.20	38.00	41.50

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	PAs	Top 17%	Top 30%
<i>Phyllomys centralis</i>	45.70	64.90	66.30
<i>Phylloscartes roquettei</i>	7.20	21.90	44.10
<i>Physalaemus atim</i>	13.10	33.10	34.70
<i>Physalaemus centralis</i>	12.80	28.80	45.80
<i>Physalaemus claptoni</i>	42.50	75.20	75.40
<i>Physalaemus deimaticus</i>	27.90	68.70	69.00
<i>Physalaemus evangelistai</i>	23.90	71.10	74.30
<i>Physalaemus marmoratus</i>	11.20	25.90	39.60
<i>Physalaemus nattereri</i>	7.80	21.30	36.60
<i>Pithecopus araguaius</i>	23.60	41.80	67.00
<i>Pithecopus ayeaye</i>	18.30	38.30	42.30
<i>Pithecopus azureus</i>	12.90	31.90	53.80
<i>Pithecopus centralis</i>	41.20	67.10	76.40
<i>Pithecopus megacephalus</i>	22.40	60.70	74.10
<i>Pithecopus oreades</i>	59.00	69.30	77.90
<i>Placosoma cipoense</i>	49.00	76.70	76.70
<i>Polystictus superciliaris</i>	18.30	45.40	58.10
<i>Porphyospiza caerulescens</i>	16.50	31.40	49.60
<i>Pristimantis dundeei</i>	21.90	38.80	56.30
<i>Pristimantis moa</i>	7.10	30.20	77.80
<i>Pristimantis ventrigranulosus</i>	5.30	28.90	36.50
<i>Proceratophrys bagnoi</i>	18.80	57.30	79.50
<i>Proceratophrys branti</i>	22.90	41.50	68.30
<i>Proceratophrys carranca</i>	0.00	35.00	39.10
<i>Proceratophrys cururu</i>	34.90	73.20	75.10
<i>Proceratophrys dibernardoi</i>	1.00	17.70	28.50
<i>Proceratophrys goyana</i>	18.70	33.50	57.60
<i>Proceratophrys huntingtoni</i>	14.50	47.60	62.80
<i>Proceratophrys moratoi</i>	8.30	18.80	25.50
<i>Proceratophrys rotundipalpebra</i>	84.60	87.30	95.20
<i>Proceratophrys salvatori</i>	44.60	52.50	66.40
<i>Proceratophrys strussmannae</i>	3.40	69.20	79.10
<i>Proceratophrys vielliardi</i>	26.50	34.60	51.80
<i>Pseudis tocantins</i>	10.50	24.90	51.50
<i>Pseudopaludicola atragula</i>	1.80	15.80	16.60
<i>Pseudopaludicola coracoralinae</i>	2.80	23.50	24.80

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	PAs	Top 17%	Top 30%
<i>Pseudopaludicola facureae</i>	0.50	10.80	16.60
<i>Pseudopaludicola ibisoroca</i>	2.00	29.80	35.90
<i>Pseudopaludicola jazmynmedonaldae</i>	56.40	85.70	87.70
<i>Pseudopaludicola mineira</i>	25.30	66.20	67.30
<i>Pseudopaludicola ternetzi</i>	18.20	30.00	44.50
<i>Psilops seductus</i>	22.90	57.00	76.60
<i>Pyrrhura pfrimeri</i>	15.80	38.80	52.60
<i>Rhachidelus brasili</i>	8.70	17.10	25.60
<i>Rhachisaurus brachylepis</i>	22.70	59.50	72.00
<i>Rhinella cerradensis</i>	16.20	25.80	56.40
<i>Rhinella inopina</i>	21.10	43.30	64.70
<i>Rhinella ocellata</i>	24.50	40.60	56.80
<i>Rhinella rubescens</i>	20.00	38.70	52.10
<i>Rhinella scitula</i>	14.90	33.80	49.40
<i>Rhinella sebbeni</i>	16.50	29.70	42.50
<i>Rhinella veredas</i>	7.70	16.80	63.20
<i>Rhipidomys ipukensis</i>	18.30	42.70	68.30
<i>Rhipidomys macrurus</i>	26.60	38.40	54.50
<i>Saltatricula atricollis</i>	10.80	22.10	36.70
<i>Salvator duseni</i>	46.70	56.80	69.70
<i>Scinax cabralensis</i>	6.60	52.10	52.80
<i>Scinax canastrensis</i>	12.50	30.20	36.10
<i>Scinax centralis</i>	7.30	22.20	34.90
<i>Scinax constrictus</i>	11.70	23.90	40.20
<i>Scinax curicica</i>	25.30	67.40	76.70
<i>Scinax goya</i>	23.30	57.70	73.60
<i>Scinax haddadorum</i>	3.10	31.60	43.50
<i>Scinax machadoi</i>	15.30	54.90	73.70
<i>Scinax maracaya</i>	26.70	46.80	48.30
<i>Scinax pinimus</i>	29.70	63.70	64.10
<i>Scinax pombali</i>	25.70	45.10	47.80
<i>Scinax rogerioi</i>	57.90	62.30	67.40
<i>Scinax rossaferesae</i>	35.80	48.20	56.70
<i>Scinax rupestris</i>	78.60	83.90	96.20
<i>Scinax skaios</i>	22.40	32.00	55.00
<i>Scinax tigrinus</i>	18.40	31.40	49.60

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Appendix S3 – Continued from previous page

	PAs	Top 17%	Top 30%
<i>Scytalopus novacapitalis</i>	22.10	34.30	43.70
<i>Siagonodon acutirostris</i>	59.80	60.40	87.80
<i>Simophis rhinostoma</i>	7.40	16.20	23.00
<i>Sporophila nigrorufa</i>	7.80	41.80	42.80
<i>Stenocercus albolineatus</i>	6.10	40.80	52.40
<i>Stenocercus canastra</i>	37.50	56.70	57.00
<i>Stenocercus quinarius</i>	31.90	42.70	74.30
<i>Stenocercus sinesaccus</i>	18.20	45.90	54.20
<i>Synallaxis simoni</i>	11.50	22.40	39.40
<i>Syndactyla dimidiata</i>	23.70	34.00	46.70
<i>Taoniscus nanus</i>	32.40	41.40	51.70
<i>Thalpomys cerradensis</i>	34.50	56.30	71.40
<i>Thalpomys lasiotis</i>	54.70	68.40	74.30
<i>Thamnodynastes rutilus</i>	28.70	35.30	47.40
<i>Thoropa megatympanum</i>	21.60	57.70	72.30
<i>Thrichomys apereoides</i>	9.10	27.60	50.40
<i>Thrichomys pachyurus</i>	33.10	44.70	63.70
<i>Thylamys velutinus</i>	45.10	58.00	61.00
<i>Trachycephalus mambaiensis</i>	25.30	39.30	56.70
<i>Trilepida brasiliensis</i>	14.90	35.50	59.40
<i>Trilepida fuliginosa</i>	12.40	23.40	47.00
<i>Trilepida jani</i>	14.50	38.60	62.20
<i>Trilepida koppesi</i>	9.40	19.90	29.70
<i>Trinomys moojeni</i>	33.30	68.00	68.40
<i>Tropidophis preciosus</i>	1.00	52.40	53.70
<i>Tropidurus callathelys</i>	20.50	54.30	54.50
<i>Tropidurus chromatops</i>	16.10	57.00	57.40
<i>Tropidurus itambere</i>	15.10	28.20	40.60
<i>Tropidurus montanus</i>	13.40	51.40	62.70
<i>Tropidurus oreadicus</i>	14.80	32.60	51.90
<i>Tupinambis matipu</i>	23.80	48.00	60.60
<i>Tupinambis quadrilineatus</i>	15.30	27.50	50.40
<i>Uropelia campestris</i>	17.30	30.10	48.60
<i>Vanzosaura savanicola</i>	30.00	39.70	72.30
<i>Xenodon matogrossensis</i>	6.20	21.30	35.70
<i>Xenodon nattereri</i>	10.80	19.30	28.60

1479

Considerações Gerais

1480 Ufa! Pra quem leu tudo (ou pelo menos um dos artigos acima) até aqui, o passeio
 1481 foi longo, tortuoso (como as belas espécies de árvore do Cerrado) e complexo, né? Se
 1482 não, que bom! Se sim, vamos lá para os principais pontos que precisam ser destacados e
 1483 lembrados daqui.

1484 Com nossos resultados, fica evidente que o conhecimento sobre a fauna de vertebrá-
 1485 dos terrestres endêmicos do Cerrado ainda tem um longo caminho pela frente. Desde o
 1486 trabalho mais recente que compilou informações sobre anfíbios anuros e répteis Squamata
 1487 endêmicos do Cerrado ([Azevedo et al., 2016](#)), 37 novas espécies foram descritas para esses
 1488 grupos. Como esperado, a maioria das espécies descritas recentemente têm distribuições
 1489 geográficas mais restritas, ou seja, podem não ter sido descritas anteriormente pelo simples
 1490 fato de não terem sido nem mesmo encontradas antes, seja por raridade intrínseca, ou por
 1491 que a região em que essas espécies ocorrem não haviam sido amostradas. Isso nos mostra
 1492 que para uma região tão ampla e diversa como o Cerrado, mesmo com trabalhos recentes
 1493 de levantamento faunístico sistemático voltados a reduzir lacunas de amostragem, ainda
 1494 há muito espaço para avanço em conhecimento taxonômico (descrição de novas espécies)
 1495 e biogeográfico (detalhamento sobre a distribuição geográfica das espécies). Em [Azevedo](#)
 1496 [et al. \(2016\)](#) a base de dados analisada tinha 216 espécies e 4588 registros únicos. Aqui,
 1497 além das 37 espécies a mais de anfíbios anuros e de répteis Squamata adicionados à base,
 1498 nós incluímos também registros de 45 espécies de aves e de 42 espécies de mamíferos.
 1499 Com isso, nossa base de dados analisada chegou a 13.800 registros únicos, conferindo um
 1500 aumento de 57% em número de espécies e de 200% em número de registros únicos anali-
 1501 sados. Com essa síntese que fizemos pudemos encontrar alguns resultados interessantes e
 1502 outros muito alarmantes.

1503 Um ponto preocupante nesse cenário é que o ritmo de avanço sobre conhecimento
 1504 taxonômico e biogeográfico não tem sido acompanhado por ações concretas direciona-
 1505 das especificamente à proteção dessas espécies, mesmo diante do cenário preocupante de
 1506 perda de habitat, nem por refinamento em escala local e global sobre as avaliações do risco
 1507 de extinção dessas espécies. Quase 87% das espécies analisadas tiveram parte da área de
 1508 suas distribuições geográficas modificadas de ambientes naturais para usos antrópicos, isso
 1509 só no período entre 2000 e 2020, com espécies que chegaram a perder até 45% de toda
 1510 sua área de distribuição. Para espécies que naturalmente possuem distribuições restritas
 1511 a pequenas áreas do globo, perder qualquer quantidade de área natural dentro de suas
 1512 áreas de distribuição já é preocupante. Considerando que muitas espécies endêmicas do
 1513 Cerrado tem alta seletividade de habitat, ou seja, ocupam majoritariamente um ou outro
 1514 tipo de vegetação típico do Cerrado, essas perdas podem ser ainda mais significativas,
 1515 especialmente se foram direcionadas ao habitat natural mais ligado à ocorrência dessas

1516 espécies. De modo geral, essa situação é mais complicada para espécies que originalmente
1517 ocorrem na porção sul do Cerrado. Isso porque nos anos 2000, quando foi publicado
1518 o trabalho clássico sobre hotspots de biodiversidade ([Myers et al., 2000](#)) essa região já
1519 havia sido amplamente modificada. Por outro lado, apesar de encontrarmos que as es-
1520 pécies restritas à porção norte do Cerrado têm proporcionalmente mais áreas de habitat
1521 natural remanescentes em suas distribuições geográficas, é nessa região onde a chapa vem
1522 esquentando nos últimos anos, com as maiores taxas de desmatamento recentes. É nesse
1523 sentido que tanto no primeiro quanto no terceiro capítulo nós chamamos a atenção para
1524 a necessidade de ampliar e criar novas unidades de conservação em porções específicas no
1525 Cerrado norte, mas sem deixar de lado a importância de tentar manter os remanescentes
1526 do Cerrado sul, propondo a criação unidades de conservação que incluam planejamento
1527 de restauração integrado ao projeto de criação.

1528 Somado a essa questão da alta perda de habitat recente, encontramos que mais de
1529 87% das espécies analisadas não têm nem 17% da suas áreas de distribuição protegidas
1530 pela rede atual de unidades de conservação de uso restrito. Esses 17%, são usados como
1531 parâmetro por que são o “alvo” estipulado na convenção sobre diversidade biológica ([CBD](#),
1532 da sigla em inglês para *Convention on Biological Diversity*) que fosse protegido, do ambi-
1533 ente terrestre global até 2020. No Cerrado estamos distantes desse alvo e apenas 10,25%
1534 são protegidos por lei, isso se considerarmos todas as categorias de unidade de conserva-
1535 ção existentes, o que cai pra pouco mais de 2,5% se considerarmos apenas as unidades
1536 de conservação de uso restrito. Como se isso não bastasse, encontramos no capítulo 3
1537 que a conversão de áreas naturais ao longo dos anos vem reduzindo nossa capacidade de
1538 representar, proporcionalmente, maiores áreas da distribuição das espécies analisadas em
1539 áreas prioritárias à conservação, isso por que estamos consideramos aqui que ao converter
1540 uma área natural para qualquer uso do solo antrópico impede a ocorrência das espécies
1541 estudadas. Isso é fato para a maioria das espécies analisadas, porém nosso conhecimento
1542 sobre os habitats preferenciais de algumas dessas espécies ainda é muito limitado, espe-
1543 cialmente para espécies que foram descritas a partir de um único indivíduo ou de uma
1544 população de uma única localidade.

1545 É nessa onda de que ainda precisamos coletar mais informações sobre algumas espé-
1546 cies que é possível justificar (mas não muito, veja a seguir) a alta quantidade de espécies
1547 avaliadas como possuindo “Dados Insuficientes” (espécies ‘*DD - Data Deficient*’, de acordo
1548 com a nomenclatura usada pela União Internacional para Conservação da Natureza, a
1549 [IUCN](#), da sigla em inglês para *International Union for Conservation of Nature and Natu-*
1550 *ral Resources*). Isso pra dizer que sim, de fato é interessante obter mais informações sobre
1551 as espécies descritas mais recentemente, porém, é de suma importância que avaliemos
1552 com mais atenção o que vem acontecendo em grande proporção dentro das distribuições
1553 dessas espécies, uma vez que especialmente espécies descritas mais recentemente, com dis-
1554 tribuições restritas e com altas taxas de perda de habitat estão atualmente classificadas

1555 como ‘DD’ (ver “[Figure 5](#)”), e isso dificulta a atribuição de pesos adequados à realidade
1556 de ameaça dessas espécies em análises sistemáticas de avaliação.

1557 Ainda no que diz respeito à avaliação de risco de extinção das espécies analisadas,
1558 encontramos discrepâncias importantes entre a lista global e a lista nacional de espécies
1559 ameaçadas. Em primeiro lugar, na quantidade de espécies avaliadas em cada lista. A
1560 lista nacional é mais completa, contendo quase 93% de todas as espécies conhecidas de
1561 Tetrapoda endêmicas do Cerrado, em comparação com os quase 78% da lista global. É
1562 preocupante que de modo geral temos mais espécies consideradas ameaçadas pela lista
1563 nacional, uma vez que é a lista global que normalmente é utilizada como referência em
1564 análises de priorização. Como, na prática, é possível que a lista global seja atualizada
1565 baseada nas listas nacionais, especialmente para espécies endêmica do Cerrado, que tem
1566 mais de 95% da sua área contida em território brasileiro, essa diferença entre as duas listas
1567 pode resultar apenas da falta de celeridade na transferência de informações entre uma
1568 lista e outra, o que pode potencialmente ser solucionado com um melhor planejamento
1569 dessa etapa. Como possibilidade de análise futura, comparar os resultados de priorização
1570 pautados nas avaliações de cada lista poderá nos dar uma dimensão mais aproximada dos
1571 impactos que essa discrepância pode trazer no que diz respeito à determinação de áreas
1572 prioritárias à conservação, e talvez ressaltar a importância de sermos mais eficientes na
1573 comunicação entre as avaliações nacionais e a disponibilidade desses dados na lista global.

1574 Ainda assim, comparando os resultados que nós encontramos com a proporção de
1575 espécies ameaçadas em cada classe de vertebrado em nível global, é possível notar que
1576 mesmo a lista mais completa de avaliação (nesse caso, a lista nacional) pode nos limitar
1577 quanto à interpretação correta sobre o risco de extinção das espécies analisadas. Isso
1578 por que não é nada trivial tentar explicar como as espécies endêmicas de um hotspot de
1579 biodiversidade, altamente impactado, também apontado como um hotspot de desmata-
1580 mento recente, podem apresentar proporcionalmente menos espécies ameaçadas do que
1581 as espécies avaliadas em todo o globo. E foi isso o que encontramos. Se fossemos usar,
1582 por exemplo, a proporção de anfíbios ameaçados globalmente para ter uma estimativa
1583 conservadora de quantas espécies endêmicas de anfíbios poderiam, proporcionalmente,
1584 serem avaliadas como ameaçadas no Cerrado, deveríamos ter um número **DOZE** vezes
1585 maior de espécies avaliadas como ameaçadas. Se repetirmos esse raciocínio, para répteis
1586 Squamata deveríamos esperar pelo menos duas vezes e meia mais espécies avaliadas como
1587 ameaçadas. Desse modo, é possível apontar que há, potencialmente, alguma limitação
1588 considerável em avaliar adequadamente o risco de extinção das espécies da herpetofauna
1589 endêmica do Cerrado. Mencionamos especificamente a herpetofauna por que para aves e
1590 mamíferos a proporção de espécies avaliadas como ameaçadas no Cerrado é maior do que
1591 a encontrada para todas as espécies avaliadas no globo, o que condiz com condição de
1592 hotspot de biodiversidade, altamente impactado e com taxas crescentes de desmatamento.

1593 Agora, sobre alguns avanços que tivemos e que podem nos ajudar a ter uma visão

1594 mais holística da composição de biotas formadas por espécies endêmicas do Cerrado. Ape-
1595 sar da sequência de capítulos apresentada, as primeiras ideias que queríamos testar nesta
1596 tese são as que foram apresentadas no capítulo 2, relacionadas aos resultados encontrados
1597 por [Azevedo et al. \(2016\)](#). Isso para testar a robustez das unidades biogeográficas que
1598 foram encontradas naquele estudo, pensando que se essas unidades se mantivessem pre-
1599 sentes com esse aumento no número de espécies e registros analisados, teríamos um sinal
1600 de que de fato essas poderiam ser consideradas válidas (pelo menos até o momento). No
1601 resumo da ópera, nós também encontramos um padrão de endemismo congruente a partir
1602 da detecção de agrupamentos não aleatórios da distribuição de espécies co-distribuídas,
1603 mas, agora para tetrapoda. Além disso, 81% das unidades detectadas por ([Azevedo et al.,](#)
1604 [2016](#)) foram recuperadas com os nossos dados, e as que não foram detectadas certamente
1605 ficaram de fora por que algumas das espécies que às compunham não são mais conside-
1606 radas espécies válidas, e essas unidades perderam o sinal biogeográfico que elas traziam.
1607 Por outro lado, nós detectamos novas unidades que ainda não haviam sido encontradas,
1608 como por exemplo as unidades da Bodoquena, os Campos Gerais no estado do Paraná e
1609 a da porção superior do vale do Guaporé. E o que essas unidades têm em comum para
1610 terem sido encontradas desta vez? Em primeiro lugar, todas elas têm pelo menos uma
1611 espécie de mamífero na sua composição, e em segundo, duas delas têm também espécies
1612 da herpetofauna descritas nos últimos anos.

1613 Isso nos mostra que, de fato, para chegarmos em algum ponto em que possamos
1614 propor unidades biogeográficas gerais e robustas, é importante tentar avaliar o maior nú-
1615 mero de espécies que tenhamos informações sobre suas distribuições, independente dessas
1616 espécies terem capacidades distintas de dispersão ou tolerâncias diferentes ao ambiente.
1617 E isso se reforça ao percebermos que mesmo as aves, que entre os grupos analisados têm
1618 a maior capacidade de dispersão, também são afetadas por fatores históricos que limi-
1619 tam a distribuição das espécies no Cerrado. Basta perceber que pelo menos um quarto
1620 das espécies de aves que formam as unidades detectadas estão em unidades classificadas
1621 como possuindo espécies de distribuições restritas e um terço formam unidades de dis-
1622 tribuições parciais. Outro componente importante desse capítulo é o fato de que essas
1623 unidades biogeográficas são formadas majoritariamente ou por espécies com distribuição
1624 altitudinal confinada nos planaltos ou confinadas nas depressões periféricas que permeiam
1625 o Cerrado, sendo que mais de 75% de todas as espécies que formam as unidades detec-
1626 tadas estão em planaltos, incluindo mais de 85% das espécies de aves e anfíbios. Com
1627 esse entendimento mais refinado sobre a composição, e localização das unidades, além da
1628 clara detecção do componente altitudinal na sua formação, temos maiores possibilidades
1629 de explorar perguntas relacionadas a delimitação dessas áreas, além de poder elaborar
1630 novos questionamentos sobre os processos envolvidos na formação da fauna endêmica e
1631 na origem do próprio Cerrado.

1632 Pra finalizar, reconhecendo a problemática relacionada às ameaças intrínsecas (e.g.

1633 distribuições restritas e seletividade de habitats) e extrínsecas (e.g. alta perda de habitat,
1634 baixa taxa de proteção) das espécies analisadas é que fechamos a tese com um capítulo
1635 com a proposição de áreas prioritárias à conservação. Originalmente, áreas que seriam
1636 prioritárias à conservação de vertebrados terrestres endêmicos do Cerrado eram espalhadas
1637 por todo seu território e formadas por áreas de habitat natural contíguas. Com o passar do
1638 tempo e com estímulos para que a região central do Brasil fosse ocupada e utilizada para
1639 o desenvolvimento econômico do país, especialmente através da agropecuária, grandes
1640 extensões de habitats naturais foram convertidas a usos antrópicos. Inicialmente esse
1641 processo acometeu principalmente a porção sul do Cerrado, de modo que já em 1985 uma
1642 vasta porção dessa região já havia sido convertida. Embora novas unidades de conservação
1643 tenham sido criadas ao longo do tempo (ver “[Figure S1](#)”), a proporção de área protegida por
1644 elas segue não sendo representativa, enquanto que a expansão agropecuária se manteve
1645 em ritmos acelerados, atualmente acometendo a região norte do Cerrado. É nesse cenário
1646 em que as maiores áreas prioritárias à conservação da fauna de vertebrados terrestres
1647 endêmicos atualmente estão concentradas na porção norte da ecoregião. Com isso das
1648 modificações na disponibilidade de áreas naturais para criação de unidades de conservação
1649 contíguas nós avaliamos o quanto era possível seguir representando essas espécies mesmo
1650 em unidades menores, e o que encontramos é que na prática, não é somente a extensão
1651 de áreas prioritárias contíguas que vem se reduzindo, mas também nossa capacidade de
1652 representar adequadamente grandes proporções das distribuições geográficas das espécies
1653 analisadas.

1654 Por outro lado, ainda podemos ser *um pouco* otimistas. Se as áreas prioritárias
1655 que encontramos forem de fato usadas para pautar a criação de unidades de conservação
1656 em tempo hábil, ainda seremos capazes de representar em média 43,5% das distribui-
1657 ções das espécies analisadas. Isso necessitando aumentar em apenas 6,75% a cobertura
1658 de unidades de conservação do Cerrado (alcançando os 17% que mencionei mais acima),
1659 o que representa aproximadamente 135.000km² do seu território. Ainda assim, embora
1660 a média das áreas de distribuição que passariam a ser representadas seja relativamente
1661 alta, haveriam espécies com apenas 10% de suas distribuições protegidas. Isso teria uma
1662 melhora significativa caso os top 30% da região fossem protegidos por unidades de con-
1663 servação, com uma média de 56,2% das distribuições dessas espécies sendo representadas,
1664 e com pelo menos 16,6% da distribuição de cada espécie sendo incluso nessas unidades
1665 de conservação (ver “[Appendix S3](#)”). O que preocupa nesse cenário é que com a taxa de
1666 desmatamento sendo mais alta que a resposta com criação de unidades de conservação
1667 essas áreas prioritárias seguirão sendo deterioradas e nossa capacidade de proteger essas
1668 espécies também. Por isso ressaltamos a necessidade de salvaguardar a áreas prioritárias
1669 com maiores extensões, localizadas no norte do Cerrado, que é onde o avanço da agrope-
1670 cuária é mais acentuado atualmente (ver [P. Pacheco et al., 2021](#)). Um ponto adicional a
1671 se considerar aqui é sobre o potencial de áreas de proteção que deveriam ser mantidas em

1672 propriedades privadas. Caso essas áreas sejam adequadamente restauradas ao ponto de se
1673 manterem/tornarem habitáveis seria possível aumentar ainda mais a representatividade
1674 de espécies de vertebrados ameaçadas no Cerrado. Assim, ampliamos o nosso leque de
1675 abordagens, para além da criação e restauração de unidades de conservação, o que pelo
1676 menos em teoria dá um respiro a mais, apesar de que seguiria sendo necessário capacitar
1677 e ampliar os esforços para fiscalização e avaliação da eficiência dessas áreas.

1678 Só um adendo ligeiro antes de fechar de vez. Você deve ter notado (ou não) que o
1679 número de espécies analisadas em cada artigo variou. Embora o total de espécies de tetra-
1680 poda endêmicas do Cerrado descritas até janeiro de 2021 seja mesmo 340, para algumas
1681 análises não foi possível incluir todas elas. Isso por que algumas das análises dependiam
1682 da disponibilidade de dados da base do MapBiomass, e nesse caso temos apenas dados
1683 para o Cerrado incluso no território brasileiro. Desse modo, duas espécies endêmicas que
1684 ocorrem no Cerrado boliviano (*Hylaeamys acritus* e *Juscelinomys huanchacae*) acabaram
1685 excluídas e isso determinou o número total de espécies e registros analisados em cada
1686 capítulo. Além dessas duas, perceba que no capítulo 3 nós excluímos também a espécie
1687 *Juscelinomys candango* da análise, mas isso por que decidimos não incluir uma espécie
1688 que é considerada extinta (pela lista global) em uma análise de prioridades de conser-
1689 vação. De todo modo, esses percalços metodológicos destacam que nossa capacidade de
1690 gerar planos sistemáticos de conservação que consideram ecorregiões inteiras na extensão
1691 que tem o Cerrado pode não ser a melhor estratégia para contemplar algumas espécies,
1692 especialmente as que ocorrem em áreas marginais dessas ecorregiões. Além disso, desta-
1693 camos o papel fundamental de listas nacionais, com olhar mais detalhado e dedicado à
1694 fauna e flora local, e a importância de criar iniciativas transfronteiriças para salvaguardar
1695 a biodiversidade.

1696 É isso... o resumo do resumo é: aprendemos muito sobre a biodiversidade de
1697 vertebrados terrestres endêmicos do Cerrado nas últimas décadas. No entanto, estamos
1698 descobrindo espécies que mal estão sendo validadas e já estão sob elevada pressão an-
1699 trópica em seus habitats confinados às suas distribuições restritas. Além disso, como as
1700 distribuições dessas espécies revelam um padrão de co-ocorrência, é possível que unidades
1701 biogeográficas inteiras, geradas por processos históricos, estejam sob risco de perderem
1702 suas espécies representativas. Logo, é possível que percamos os sinais biogeográficos que
1703 essas espécies nos fornecem e, consequentemente, perdemos nossa capacidade de entender
1704 de modo mais aprofundado a origem do Cerrado e de sua riquíssima fauna e flora. E,
1705 a menos que ajamos de forma planejada e célere vamos cada vez mais ser limitados na
1706 nossa capacidade de conter a extinção de diversas espécies de animais e plantas na maior
1707 e mais ameaçada savana do planeta.

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Registro de um dia chuvoso no Morro do Fumo, localidade tipo da espécie de lagarto endêmico *Bachia oxyrhina* ($10^{\circ}51'58.41''S$, $46^{\circ}49'9.07''W$), na Estação Ecológica Serra Geral do Tocantins.