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FÁBIO JÚLO ALVES BORGES

TESE DE DOUTORADO

Prioridades para a conservação de aves no Cerrado diante das mudanças globais

Orientador: Prof. Dr. Rafael Loyola

Goiânia – GO

Março 2020

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Fábio Júlio Alves Borges

TESE DE DOUTORADO

Prioridades para a conservação de aves no Cerrado diante das mudanças globais

Tese apresentada à Universidade Federal de Goiás, como parte das exigências do Programa de Pós-graduação em Ecologia e Evolução para obtenção do título de Doutor.

Orientador: Prof. Dr. Rafael Loyola

Goiânia – GO

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ATA DE DEFESA DE TESE

Ata nº 98 da sessão de Defesa de Tese de **Fábio Júlio Alves Borges**, que confere o título de **Doutor em Ecologia e Evolução**, na área de concentração em **Ecologia e Evolução**.

Aos **trinta dias do mês de março de dois mil e vinte (30/03/2020)**, a partir das **14h00min**, por **videoconferência**, seguindo portaria CAPES no. 36 de 16 de março de 2020 e recomendação da UFG, realizou-se a sessão pública de Defesa de Tese intitulada **“Prioridades para a conservação de aves no Cerrado diante das mudanças globais”**. Os trabalhos foram instalados pelo Orientador, **Prof. Dr. Rafael Loyola - Depto Ecologia/UFG**, com a participação dos demais membros da Banca Examinadora: **Prof. Dr. Paulo De Marco Júnior - Depto Ecologia/UFG**, membro titular interno; **Profa. Dra. Levi Carina Terribile - Depto Ciências Biológicas/UFJ**, membro titular interno; **Prof. Dr. Roberto Brandão Cavalcanti - Depto de Zoologia/UnB**, membro titular externo; e **Dra. Fernanda Thiesen Brum - PPG em Ecologia e Conservação/UFPR**, membro titular externo. Durante a arguição os membros da banca não fizeram sugestão de alteração do título do trabalho. A Banca Examinadora reuniu-se em sessão secreta a fim de concluir o julgamento da Tese, tendo sido o candidato **APROVADO** pelos seus membros. Proclamados os resultados pelo **Prof. Dr. Rafael Loyola**, Presidente da Banca Examinadora, foram encerrados os trabalhos e, para constar, lavrou-se a presente ata que é assinada pelos Membros da Banca Examinadora, ao(s) **trinta dias do mês de março de dois mil e vinte (30/03/2020)**.

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*Dedico esta tese a minha família, meus pais
Lindionor e Maria Divina por todo amor, carinho,
dedicação e orações, meus irmãos Ângela e Elton
por todo apoio e torcida tão fundamentais.*

It seems to me that the natural world is the greatest source of excitement,
the greatest source of visual beauty,
the greatest source of intellectual interest.
It is the greatest source of so much in life that makes life worth living.

(David Attenborough)

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Resumo

As mudanças climática e de uso da terra têm afetado os ecossistemas naturais, reduzindo e fragmentando o habitat disponível para as espécies, aumentando o isolamento das populações e, conseqüentemente, diminuindo o fluxo gênico, mudando a distribuição das espécies, alterando seus ciclos de vida, causando declínios populacionais e extinção de espécies. São apontadas com as pressões diretas mais importantes sobre a biodiversidade terrestre e seus impactos tendem a aumentar nas próximas décadas. Neste contexto, um estudo para o planejamento de conservação que apresente os mecanismos de resposta das espécies, indique as espécies que estarão mais vulneráveis, aponte áreas importantes para a conservação das espécies e discuta como os diferentes componentes da diversidade serão afetados por estas mudanças torna-se necessário e importante. O Cerrado é considerado a savana mais vulnerável do mundo. Praticamente 50% da sua cobertura de vegetação nativa foi perdida e apenas 7,5% do Cerrado é coberto por áreas protegidas. Além disso, é projetado um aumento de temperatura de 5 a 5,5°C e uma redução na precipitação de 35 a 45% para o Cerrado até o final deste século, o que coloca em risco toda sua biodiversidade. Esta tese avaliou os possíveis impactos das mudanças climática e de uso da terra para as aves no Cerrado e apresenta propostas de conservação diante de tais impactos. O capítulo 1 traz uma revisão da literatura que busca encontrar os possíveis mecanismos de resposta das espécies à mudança climática através de seus atributos biológicos e ecológicos. O capítulo 2 apresenta uma avaliação da vulnerabilidade das espécies à mudança climática e de uso da terra, considerando a sensibilidade, a capacidade adaptativa e a exposição das espécies avaliadas. Ainda, é apresentado um mapeamento dos componentes da vulnerabilidade e o quanto da distribuição de cada espécie mais vulnerável está dentro das áreas protegidas. O capítulo 3 apresenta as áreas onde as condições climáticas mudariam pouco e manteriam a vegetação nativa, podendo atuar

como refúgios para as espécies. Apresenta uma estimativa da proporção da distribuição das espécies que ocorrerá dentro das áreas de refúgio. Apresenta e discute estratégias de conservação mais adequadas para proteger as espécies nas áreas com diferentes combinações de clima e uso da terra. O capítulo 4 mostra como a estrutura funcional e filogenética das comunidades de aves estão relacionadas com a riqueza de espécies e como esses componentes estão distribuídos espacialmente no Cerrado. Além disso, traz uma avaliação de como as mudanças climáticas e de uso da terra irão afetar as estruturas funcionais e filogenéticas, apresenta o mapeamento de áreas importantes para proteger os componentes taxonômico, filogenético e funcional, avaliando a congruência espacial entre essas áreas.

Palavras-chave: Mudança climática, Mudança no uso da terra, Vulnerabilidade, Refúgios, Estratégias de conservação, Diversidade filogenética, Diversidade funcional, Homogeneização biótica.

Abstract

Climate and land use changes are affecting natural ecosystems, reducing and fragmenting the habitat available to species, increasing population isolation and, consequently, decreasing gene flow, changing species distribution, altering their life cycles, causing population declines and species extinction. They are pointed out with the most important direct pressures on terrestrial biodiversity and their impacts tend to increase in the coming decades. In this context, a study for conservation planning that presents the response mechanisms of the species, indicates the species that will be most vulnerable, identifies the most important areas for the conservation of the species and discuss how the different components of diversity will be affected by these changes becomes necessary and important. The Cerrado is a biodiversity hotspot, being considered the most vulnerable savanna in the world. Virtually 50% of its native vegetation cover has been lost and only 7.5% of the Cerrado is covered by protected areas. In addition, a temperature increase of 5 to 5.5°C and a reduction in precipitation of 35 to 45% for the Cerrado are projected by the end of this century, which puts all of its biodiversity at risk. This thesis assesses the possible impacts of climate and land use changes for birds in the Cerrado and presents conservation proposals in the face of such impacts. Chapter 1 provides a literature review that seeks to find possible mechanisms for species response to climate change through their biological and ecological traits. Chapter 2 makes an assessment of species vulnerability to climate and land use changes, considering sensitivity, adaptive capacity and exposure of the species evaluated. Still, a mapping of these components is presented and how much of the distribution of each most vulnerable species is within the protected areas. Chapter 3 identifies areas where climatic conditions would change little and maintain native vegetation, which could act as refugia for species. Estimates the

proportion of species distribution that will occur within the areas of refugia. It presents and discusses the most appropriate conservation strategies to protect species in areas with different combinations of climate and land use. Chapter 4 shows how the functional and phylogenetic structure of bird communities is related to species richness and how these components are spatially distributed in the Cerrado. In addition, it assesses how climate and land use changes will affect functional and phylogenetic structures, maps important areas to protect taxonomic, phylogenetic and functional components and assesses the spatial congruence between these areas.

Keywords: Climate change, Land use change, Vulnerability, Refugia, Conservation strategies, Phylogenetic diversity, Functional diversity, Biotic homogenization

Apresentação

Esta tese busca descrever como as mudanças climáticas e de uso da terra projetadas até 2050 poderiam afetar as espécies de aves no Cerrado brasileiro, apresentando estratégias de conservação com o objetivo de mitigar seus impactos. Dessa forma, nesta tese apresento uma discussão dos mecanismos de respostas dos atributos das espécies, avalio aspectos da vulnerabilidade das espécies, identifico áreas importantes para a conservação das espécies e exploro os impactos nos três componentes da diversidade (taxonômico, filogenético e funcional). Esta tese está dividida em quatro capítulos estruturados no formato de artigos científicos. Cada capítulo segue a formatação da revista a qual foi submetido. O capítulo 1 foi formatado nas normas da revista *Oecologia*, o capítulo 2 está publicado na *Biological Conservation*, o capítulo 3 está aceito na *Perspectives in Ecology and Conservation* e o capítulo 4 foi formatado nas normas da *Biodiversity and Conservation*. Com exceção do capítulo 1, que traz uma abordagem global, multi taxonômica e avalia apenas os impactos da mudança climática, os demais capítulos avaliam também a mudança no uso da terra com o foco para aves no Cerrado.

O capítulo 1 apresenta uma revisão da literatura com o objetivo de descrever os mecanismos pelos quais o tamanho da ninhada, amplitude da dieta, capacidade de dispersão e tolerância climática influenciam a reposta das espécies à mudança climática. Os resultados indicam que as espécies que habitam regiões tropicais e temperadas apresentam diferentes mecanismos de resposta às mudanças climáticas. Enquanto espécies de regiões temperadas podem responder positivamente ao aumento de temperatura, espécies dos trópicos podem ser severamente afetadas. Como os ectotérmicos dependem da temperatura ambiente, são mais sensíveis e apresentam mecanismos de resposta diferentes dos endotérmicos.

O capítulo 2 traz uma avaliação da vulnerabilidade de um conjunto de 103 espécies de aves às mudanças climática e de uso da terra considerando sua sensibilidade, capacidade adaptativa e exposição. Os resultados mostram que 67%, 71% e 39% das espécies foram sensíveis, tinham baixa capacidade adaptativa e foram expostas, respectivamente. 25% das espécies foram classificadas como altamente vulneráveis. Entre essas espécies, 10 estão atualmente ameaçadas no Brasil. A rede de áreas protegidas abriga uma pequena extensão da distribuição das espécies altamente vulneráveis, com 19 espécies (73%) tendo menos de 10% de suas distribuições dentro das áreas protegidas.

O capítulo 3 apresenta áreas que potencialmente podem servir como refúgios (baixa anomalia climática e manutenção da vegetação nativa) e áreas de alto risco (alta anomalia climática e perda da vegetação nativa) para as espécies, combinando medidas de anomalia climática com um modelo de uso da terra, ambos projetados para 2050. Os resultados indicam que apenas 13% do Cerrado podem servir de refúgio para as espécies de aves. Por outro lado, quase 35% do bioma podem se tornar áreas de alto risco para essas espécies. A maioria das espécies (74%) apresentam de 34% a 85% de sua distribuição geográfica em áreas com pouca vegetação nativa, mas com baixa anomalia climática. São apresentadas e discutidas diferentes estratégias de conservação para cada uma das áreas identificadas no estudo.

Por fim, o capítulo 4 apresenta uma avaliação do padrão atual das relações entre os três componentes da diversidade e discute como as mudanças climáticas e de uso da terra poderão afetar a diversidade taxonômica, filogenética e funcional das comunidades de aves no Cerrado. Os resultados mostram que a diversidade filogenética foi positivamente relacionada a diversidade taxonômica, enquanto a diversidade funcional mostrou uma relação negativa. No geral, houve uma alta incongruência espacial entre os três componentes da diversidade. Foram encontrados maiores valores de diversidade beta (turnover) para os três componentes na zona de transição entre o Cerrado e Amazônia, no restante do Cerrado os valores foram baixos. Devido às mudanças climática e de uso da terra poucas áreas perderiam a maioria das espécies, enquanto a maior parte do Cerrado perderia poucas espécies. As comunidades de aves se tornarão mais agrupadas filogeneticamente e funcionalmente no futuro e poucas áreas poderão proteger simultaneamente a diversidade filogenética e funcional.

Introdução geral

Atualmente os profissionais da conservação e os tomadores de decisão enfrentam a difícil tarefa de tentar proteger as espécies diante de múltiplas ameaças, incluindo as mudanças climáticas e de uso da terra. Mudanças climáticas e de uso da terra estão afetando os ecossistemas naturais, reduzindo o habitat disponível para as espécies e causando extinções de espécies e perda de biodiversidade (Steffen et al., 2007). São apontadas como as pressões diretas mais prejudiciais à biodiversidade terrestre e seus impactos tendem a aumentar nas próximas décadas (WWF, 2014; Newbold et al., 2019; Tilman et al., 2017). Além disso, essas duas ameaças podem promover a homogeneização da biodiversidade terrestre, trazendo consequências para o funcionamento dos ecossistemas e do bem-estar humano (Newbold et al., 2019). Até o momento, a mudança no uso da terra (perda e degradação de habitats) é considerada o principal impacto humano na ameaça à biodiversidade (Haddad et al., 2015; Hanski et al., 2013; Newbold et al., 2015; Pereira et al., 2012; Wilcove et al., 1998). No entanto, as mudanças climáticas se tornarão mais acentuadas no futuro próximo e é esperado que seus efeitos excedam os impactos das mudanças de uso da terra em meados deste século (Newbold, 2018). Seguindo as trajetórias atuais, as mudanças climáticas e de uso da terra combinadas podem levar a uma perda média de até 38% das espécies nas comunidades globalmente (Newbold, 2018). Nos trópicos, apenas a expansão futura do uso da terra poderá causar uma perda de 30% na riqueza e de 31% na abundância das espécies (Kehoe et al., 2017). Por outro lado, a mudança climática sozinha poderá levar a uma perda de mais de 50% da área de distribuição de mais da metade das espécies globalmente (Warren et al., 2018).

Muitos declínios populacionais e de espécies podem ser atribuídos à destruição e fragmentação do habitat e mudanças no uso da terra (Fahrig, 2003; Vitousek et al., 1997). A mudança no uso da terra afeta a biodiversidade e os ecossistemas, não apenas reduzindo o tamanho e movimentos da população, mas também reduzindo a área do habitat, aumentando o isolamento e a borda do habitat (Haddad et al., 2015). Reduzir a área ou aumentar o isolamento diminui a persistência e a riqueza de espécies (Haddad et al., 2015). Globalmente, os habitats naturais estão sofrendo destruição, fragmentação e superexploração de recursos naturais (Fahrig, 2003). Estradas, rodovias, ferrovias, agricultura intensiva e desenvolvimento urbano estão transformando a paisagem em fragmentos pequenos e isolados, muitas vezes incapazes de suportar altos níveis de biodiversidade (EAA, 2011). Para algumas espécies, esses fragmentos não conseguem

fornecer uma área mínima para sustentar uma população viável (Dover and Settele, 2009). Em escala local, as mudanças no uso da terra causam reduções de 75% na riqueza de espécies e de 40% na abundância de organismos em habitats impactados pela ação humana em comparação com habitats não perturbados (Murphy and Romanuk, 2014; Newbold et al., 2015). Como resultado da alta proporção da superfície terrestre usada pelos seres humanos, estima-se que as comunidades ecológicas tenham perdido algo entre 13% e 25% de suas espécies (Newbold et al., 2016, 2015).

Fragmentação, redução e isolamento com seus impactos concomitantes sobre espécies e comunidades em termos de tamanho, qualidade e conectividade de habitat, são os efeitos mais notáveis das mudanças no uso da terra (Dover and Settele, 2009; Fahrig, 2003). Grandes distâncias entre os fragmentos de habitat reduzem as taxas de colonização e os eventos de dispersão (Fahrig, 2003). O isolamento de habitats geralmente aumenta o risco de impactos adversos, levando potencialmente à extinção de espécies, incluindo depressão por endogamia (Habel and Schmitt, 2012; Nieminen et al., 2001). O tamanho do fragmento claramente é um fator importante que influencia a biodiversidade. Em grandes áreas de habitat, é mais provável que populações de fontes estáveis se estabeleçam, enquanto populações em áreas menores podem apresentar riscos de extinção mais altos (Fischer and Lindenmayer, 2007; Remeš, 2000). Além disso, manchas menores de habitat são mais suscetíveis a impactos ambientais devido à sua maior proporção de bordas (Fahrig, 2003). Embora o tamanho e o grau de isolamento do fragmento sejam importantes para a sua ocupação, o tipo de uso da terra na matriz circundante afeta fortemente a sensibilidade das espécies na ocupação do habitat (Prugh et al., 2008).

As mudanças climáticas podem afetar as espécies de várias maneiras. Muitas espécies estão mudando suas distribuições, alterando o tempo dos eventos de seus ciclos de vida, como migração, reprodução e eclosão, perdendo espécies usadas como mutualistas ou recursos, sofrendo aumento da competição por espécies invasoras ou patógenos, perdendo pistas ambientais, reduzindo sua fecundidade e fitness, mudando suas proporções sexuais e populações locais estão sendo extintas (Beever et al., 2003; Cahill et al., 2013; Crick and Sparks, 1999; Foden et al., 2008; Parmesan, 2006; Parmesan and Yohe, 2003). Espera-se que esses impactos se intensifiquem, uma vez que as projeções climáticas indicam um aumento na temperatura global de cerca de 4,8 °C até o final deste século, dependendo do cenário de emissão de gases de efeito estufa (IPCC, 2013).

Ao afetar as tolerâncias térmicas das espécies, as mudanças climáticas podem resultar diretamente em extinções locais. Segundo Sinervo et al. (2010), 20% de todas as espécies de lagartos podem estar ameaçados de extinção em 2080, devido à perda de seu nicho térmico. Estudos com borboletas sugerem que aproximadamente metade das extinções recentes em nível de população provavelmente foram causadas por mudanças climáticas (Thomas et al., 2006). Sem surpresa, as primeiras extinções de espécies inteiras atribuídas ao aquecimento global foram registradas para espécies restritas as montanhas, incapazes de lidar com o aumento da temperatura ou de ajustar suas distribuições geográficas (Parmesan, 2006).

As espécies estão alterando sua fenologia como resposta às mudanças climáticas. Plantas estão antecipando sua floração, várias espécies animais estão aparecendo mais cedo e exibindo avanços em suas atividades reprodutivas (Parmesan, 2006). De acordo com um estudo multi-taxonômico, 59% de 1598 espécies estudadas exibiram mudanças em suas fenologias (Parmesan and Yohe, 2003). Uma análise mais aprofundada das respostas fenológicas resultou em estimativas de um aparecimento anterior médio de 2,3 dias por década (Parmesan and Yohe, 2003). No Reino Unido, as datas médias de postura das primeiras ninhadas para 20 espécies de aves avançaram em média 8,8 dias entre 1971 e 1995 (Crick et al., 1997). Na Grã-Bretanha, a maioria das espécies de borboletas avançou significativamente seu aparecimento nos últimos 30 anos (Diamond et al., 2011). Além da resposta individual, as mudanças climáticas também devem afetar as interações entre espécies e a composição das comunidades (Devictor et al., 2012). As interações predador-presa, planta-inseto ou parasita-hospedeiro podem ser interrompidas quando as espécies respondem diferentemente às mudanças climáticas (Parmesan, 2006; Visser and Both, 2005).

Os efeitos das mudanças climáticas e de uso da terra sobre a biodiversidade podem ser maiores do que se pensava anteriormente, pois elas podem interagir de várias maneiras (Mantyka-Pringle et al., 2012; Newbold et al., 2019; Oliver and Morecroft, 2014). Além disso, as evidências sugerem que as respostas da biodiversidade às mudanças no clima e no uso da terra são desiguais, com variação entre espécies e regiões geográficas (Foden et al., 2013; Newbold, 2018; Newbold et al., 2018). Efeitos interativos e respostas desiguais provavelmente levarão a resultados imprevistos para a biodiversidade (Newbold et al., 2019). A mudança climática pode afetar a maneira como as espécies respondem à mudança no uso da terra. Foi demonstrado que regiões com maiores aumentos de temperatura e diminuição da precipitação experimentam os maiores

impactos da perda e fragmentação de habitats (Mantyka-Pringle et al., 2012; Oliver et al., 2016). A mudança climática também pode afetar o tamanho da população, os sistemas de reprodução, as proporções sexuais e a aptidão individual, o que pode afetar a capacidade de uma espécie de responder à mudança no uso da terra (Opdam and Wascher, 2004; Verboom et al., 2010). A mudança no uso da terra pode afetar a maneira como as espécies respondem à mudança climática. A mudança no uso da terra e a fragmentação de habitats podem criar uma paisagem hostil que dificulta a capacidade das espécies de acompanhar as mudanças no clima (Eigenbrod et al., 2015; Oliver et al., 2017; Schloss et al., 2012). A mudança no uso da terra também pode levar a mudanças climáticas localizadas, com habitats antropizados geralmente mais quentes e secos que os habitats naturais (Frishkoff et al., 2015; Senior et al., 2017). Por outro lado, habitats de alta qualidade, como florestas com copas mais densas, podem amortecer o efeito da mudança climática e podem atuar como importantes refúgios para espécies sensíveis à variação climática (Jarzyna et al., 2016; Sunday et al., 2014; Terraube et al., 2017).

Devido aos seus atributos intrínsecos e capacidades de adaptação, as espécies respondem diferentemente às mudanças climáticas e de uso da terra (Borges et al., 2019; Foden et al., 2013; Maggini et al., 2014), dificultando as ações de conservação. O manejo de espécies diante das mudanças climáticas e de uso da terra requer uma compreensão de quais espécies estarão mais suscetíveis e quais fatores aumentarão sua vulnerabilidade. Vulnerabilidade é definida como a predisposição a ser negativamente afetado (IPCC, 2014), e pode ser avaliada em função da sensibilidade, capacidade adaptativa e exposição de uma espécie. A sensibilidade de uma espécie é caracterizada pela sua capacidade de suportar as mudanças, geralmente está relacionada a atributos da história de vida como a tolerância fisiológica e a especialização de habitat. A capacidade adaptativa se refere a capacidade da espécie em lidar com a mudança climática, seja adaptando-se à novas condições locais, seja dispersando-se para áreas mais adequadas. A exposição, em contrapartida, é determinada pela taxa e magnitude da mudança climática e de uso da terra experimentada pelas espécies (Dawson et al., 2011; Foden et al., 2013). Considerando sensibilidade, capacidade adaptativa e exposição, as avaliações de vulnerabilidade podem identificar quais espécies estarão mais vulneráveis, porque essas espécies estarão vulneráveis e quais fatores poderiam potencialmente reduzir sua vulnerabilidade (Böhm et al., 2016; Borges et al., 2019; Foden et al., 2013).

Diante das ameaças das mudanças climáticas e do uso da terra, uma estratégia importante para a proteção da biodiversidade é identificar áreas climáticas adequadas que

manterão habitats preservados para as espécies no futuro. Uma abordagem para identificar esses locais consiste no uso de métricas de mudança climática para a identificação de regiões que estão mais ou menos expostas a essas mudanças ao longo do tempo (Beaumont et al., 2011; Garcia et al., 2014; Loarie et al., 2009; Williams et al., 2007). A identificação e proteção de potenciais refúgios nas paisagens é uma estratégia importante para o planejamento de conservação no contexto das mudanças climáticas e de uso da terra (Groves et al., 2012; Morelli et al., 2016; Ribeiro et al., 2018; Stralberg et al., 2018; Struebig et al., 2015). A ocorrência das espécies é fortemente afetada pelo clima e sua sobrevivência depende da disponibilidade de seus habitats adequados, portanto, as espécies podem enfrentar grandes riscos se as condições climáticas às quais estão adaptadas e seus habitats adequados desaparecerem no futuro (Mantyka-Pringle et al., 2012; Newbold et al., 2015).

A forma como as espécies respondem às mudanças no clima e no uso da terra pode alterar não só a composição de espécies, mas consequentemente as estruturas filogenéticas e funcionais das comunidades e, potencialmente, poderia afetar o fornecimento de serviços ecossistêmicos (Arnan et al., 2018; Flynn et al., 2011; Hidasi-neto et al., 2019; Liang et al., 2019; Nowakowski et al., 2018; Thuiller et al., 2014). Essas mudanças globais podem atuar como um filtro capaz de reduzir as diversidades taxonômica, filogenética e funcional das comunidades levando a homogeneização biótica (Clavel et al., 2011; Newbold et al., 2019). A homogeneização biótica é um processo que leva ao aumento da similaridade entre as comunidades ao longo do tempo através da substituição sistemática de espécies de distribuição restrita por espécies amplamente distribuídas, reduzindo a diversidade espacial (McKinney and Lockwood, 1999; Olden, 2006). Esse processo pode acarretar graves consequências ecológicas e evolutivas capazes de afetar o funcionamento, estabilidade e adaptabilidade dos ecossistemas impactados (Clavel et al., 2011; Nowakowski et al., 2018; Olden et al., 2004). Já foi demonstrado que as mudanças climáticas e de uso da terra podem provocar uma redução simultânea das diversidades taxonômica, filogenética e funcional (Hidasi-neto et al., 2019; Liang et al., 2019; Thuiller et al., 2014). No entanto, a homogeneização filogenética e funcional das comunidades pode ser parcialmente motivada por diferentes mecanismos ecológicos da homogeneização taxonômica (Devictor et al., 2008; Olden, 2006). Além disso, a resposta das espécies às mudanças globais possui um forte agrupamento filogenético, de modo que certos clados são mais vulneráveis do que outros (Frishkoff et al., 2014; Nowakowski et al., 2018). Dessa forma, as mudanças climáticas e de uso da

terra podem reduzir a diversidade filogenética e a diversidade funcional das comunidades mesmo que a diversidade taxonômica permaneça quase inalterada (Arnan et al., 2018; Flynn et al., 2009; Nowakowski et al., 2018).

As espécies tropicais são particularmente vulneráveis as mudanças climática e de uso da terra, uma vez que elas já vivem próximas de seus limites máximos de tolerância térmica (Araújo et al., 2013; Khaliq et al., 2014) e possuem alta sensibilidade e baixa capacidade de adaptação (Foden et al., 2013). Além disso, a capacidade de resposta futura das espécies tropicais às mudanças globais, pode ser prejudicada devido a sua menor capacidade de dispersão (Moore et al., 2008) e menor tolerância a variação climática como resultado da evolução em um clima relativamente estável (Newbold et al., 2016; Pacifici et al., 2017). Como as condições climáticas nos trópicos devem exceder a variabilidade histórica até o final deste século (Mora et al., 2013), e rápidas mudanças no uso da terra e o crescimento da população humana são previstos em muitos cenários (Lewis et al., 2015; Popp et al., 2017), a conservação da biodiversidade na região tropical representa um grande desafio (Corlett, 2012).

O Cerrado está localizado em uma região de alta instabilidade climática futura e alta degradação da vegetação natural, podendo apresentar grandes concentrações de espécies vulneráveis (Watson et al., 2013). Projeções climáticas para o Cerrado indicam um aumento na temperatura de 5 a 5,5° C e uma diminuição no regime de chuva entre 35% e 45% até o final deste século (PBMC, 2013). Cerca de 31% a 34% da vegetação nativa remanescente do Cerrado poderá ser perdida até 2050 principalmente devido à baixa proteção e à alta pressão para expansão agrícola (Soares-Filho et al., 2016; Strassburg et al., 2017). Além disso, as áreas protegidas cobrem 7,5% do Cerrado, das quais apenas 3% são de proteção integral (Françoso et al., 2015; Strassburg et al., 2017). Como consequência da degradação ambiental poderá ocorrer a redução das formações florestais e aumento das formações abertas, reduzindo o porte e a densidade de árvores nas fitofisionomias do bioma (PNAMC, 2016). As mudanças no uso da terra no Cerrado, frequentemente associadas ao aumento da frequência de incêndios e invasão de espécies exóticas, geram profundas mudanças na estrutura da vegetação e no funcionamento de seus ecossistemas (Bustamante et al., 2012).

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Searching for synthetic mechanisms on how biological traits mediate species responses to climate change

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Abstract

Climate change will likely be the greatest challenge faced by species in this century and species ability to cope with climate change depend on their own life-history, ecological, and evolutionary traits. Understanding how these traits mediate species' responses is extremely useful to identify species that are more vulnerable or prone to extinction risk. Here, we carried out a literature review focused on describing how four traits commonly used in vulnerability assessments (i.e. clutch size, diet breadth, dispersal ability, and climatic tolerance) may actually determine species vulnerability. We also portray the possible mechanisms that explain how these traits govern species responses to climate change. The literature suggests different mechanisms operating for the evaluated traits. The mechanism of response to climate change differ between species inhabiting tropical and temperate regions: while species from temperate regions may respond positively to temperature rise, tropical species may be severely affected. Since ectotherms depend on environment temperature, they are more sensitive and present different response mechanisms from endotherms.

Keywords: Global warming; extinction risk; phenology; physiology; species traits; vulnerability assessment

Introduction

Climate change will likely be the greatest challenge faced by species this century. The observed effects include changes in distribution areas, phenology, morphology, demography and abundance (Parmesan and Yohe 2003; Parmesan 2006; Lane et al. 2012). Species ability to respond to climate change depend on their life history traits (Végvári et al. 2010; Angert et al. 2011; Pacifici et al. 2017), which can help predict species that will be more vulnerable and direct conservation efforts (Foden et al. 2013).

In this sense, the use of trait-based Climate Change Vulnerability Assessments (CCVAs) has become popular in studies that assess climate change impact on species vulnerability (Foden et al. 2018). In the context of CCVAs, the term “trait” refers to a wide range of species characteristics (such as diet breadth and climatic tolerance), instead of referring to specific characteristics of an individual (*sensu* Violle et al. 2007). Trait-based CCVAs combine scores based on exposure to climate change (extrinsic factors) with biological characteristics of species (intrinsic factors), which define their sensitivity and adaptive capacity in order to obtain a general measure of vulnerability (Pacifici et al. 2015).

Vulnerability is assessed based on these three components: exposure, sensitivity and adaptive capacity, so that species with high exposure, high sensitivity and low adaptive capacity will be the most vulnerable to climate change (Dawson et al. 2011; Foden et al. 2013). Exposure is determined by the rate and magnitude of climate change within the species’ distribution area. Sensitivity is characterised by the ability to tolerate climate change and is generally associated to traits such as physiological tolerance and habitat specialisation. Adaptive capacity refers to the ability of a given species to deal with climate change, whether adapting to new local conditions or dispersing to areas that are more suitable (Dawson et al. 2011).

Despite the importance of biological traits in determining species vulnerability, there is no agreement on which traits should be used in assessments, and their selection depends on data availability and on the opinion of experts (Foden et al. 2013, 2018). Biological traits may help identify species with higher extinction risk (Mckinney 1997; Purvis and Hector 2000). However, species responses depend on the type of threat they are exposed to (González-Suarez et al. 2013). Species that present larger body size are more threatened by hunting, while smaller and ecologically specialised species are more

threatened by habitat loss and fragmentation (Owens and Bennett 2000; González-Suarez et al. 2013).

Under the threat of climate change, biological traits might play a fundamental role in species responses, influencing their vulnerability (Jiguet et al. 2007; Angert et al. 2011; Estrada et al. 2015). Clutch size is strongly influenced by climatic variables (Jetz et al. 2008), and species may present rapid physiological adjustments of this trait in response to climatic changes (Baker 1995; Coe and Rotenberry 2003). Species that reproduce frequently or prematurely, with high fecundity, should have greater opportunities to colonise new environments (Angert et al. 2011). Species with generalist diets can change their feeding habits to other resources when climate affects the availability of preferred items (Rubolini et al. 2003; Bojarska and Selva 2012) and, consequently, they might have higher ability to change their distributions to follow suitable climatic conditions (Angert et al. 2011). Dispersal ability is a crucial trait that allows species to change their distribution areas to follow suitable climate, and species with higher dispersal ability might respond more quickly to climate change, facing lower extinction risk (Pöyry et al. 2009; Corlett and Westcott 2013). Species that are able to physiologically tolerate higher climatic variation and live in environments in which temperatures are far from their upper thermal limit will be more likely to persist under climate change (Deutsch et al. 2008; Huey et al. 2012). There is a growing interest in the use of biological traits to assess species vulnerability in response to climate change (Gardali et al. 2012; Foden et al. 2013; Garcia et al. 2014; Böhm et al. 2016; Reside et al. 2016; Borges et al. 2019). However, potentially important traits from some taxa are still frequently unavailable, which leads to the use of morphological proxies, measurements from congeneric species or the knowledge of experts (Foden et al. 2013, 2018).

Identifying the most informative traits and how they respond to climate change is a priority if we want to assess vulnerability of different species groups. However, a recent review has shown that less than half of the studies that evaluated the relationship between traits and changes in species distributions have specified hypothesis for the ecological processes involved in the relationship (Estrada et al. 2016). In order to advise appropriate conservation measures it is important to explain the reasons for choosing traits and the specific mechanisms that underlie the impacts of climate change on species of interest (Foden et al. 2018).

Here, we did a literature review aiming to understand how four traits (clutch size, diet breadth, dispersal ability and climatic tolerance), commonly used in CCVAs (Gardali

et al. 2012; Reside et al. 2016; Borges et al. 2019), might determine species vulnerability. We also aimed to describe the possible mechanisms that explain how traits influence species responses to climatic changes. Specifically, our goals were: 1) to verify whether it is possible to use the four chosen traits to understand the mechanisms underlying the impacts caused by climate change based on the ecology literature produced so far, and 2) to present and explain the main mechanisms found. Including details regarding these mechanisms will help substantiate trait choice and broaden the discussion about future conservation strategies of assessed species.

Methods

We searched the literature for studies that evaluated variation in the four aforementioned traits in response to recent climate change regarding organisms from any taxa within any level (population, community, and ecosystem). The search was carried out in July 2019 in Thomson Reuters ISI Web of Science online database and included articles published between 1945 and 2019, using the following search terms: (“trait” OR “clutch size” OR “diet” OR “dispersion” OR “climatic tolerance” OR “thermic tolerance” OR “heat tolerance”) AND (“climate change” OR “global warming” OR “temperature increase”).

We excluded studies that: (1) belonged to Web of Science categories not related to ecology (*eg.* agronomy, veterinary medicine, tropical medicine), (2) did not relate (directly or indirectly) possible trait changes to climate change, and (3) did not present any explanation to the mechanisms involved in the observed responses (*eg.* changes in distribution areas, phenology and abundance). Studies cited by the articles obtained in our search were also included in our synthetic review if they fulfilled the requirements.

Results and Discussion

Clutch size

Clutch size is one of the best-studied life history traits in birds and its variation throughout the latitude gradient is well known, with larger clutch size in higher latitudes (Lack 1947; Skutch 1949; Ashmole 1963; Ricklefs 1980; Evans et al. 2005; Jetz et al. 2008). As expected, studies that assess clutch size are focused on birds and have been carried out mainly in the temperate region (Table 1). Birds that inhabit temperate and

tropical regions adopt different life history strategies, so then can respond to climate change through different mechanisms (Table 1).

Clutch size is related to species fecundity; thus, it indicates population ability to recruit. Species with smaller clutch size present low reproductive potential and consequently a slower response to risk factors, which would make them more vulnerable to decline and extinction (Smith and Quin 1996; Pimm 1991; Hero et al. 2005). On the other hand, species with larger clutch size may present higher ability to respond to climate change, for they present shorter life cycles (Mckinney 1997). Larger clutch size is related to the probability of occupying broader geographic areas, higher dispersal ability and higher ability to colonise changing habitats and explore new opportunities (Duncan et al. 2001; Hero et al. 2005).

Some studies have found a significant relationship between clutch size and environmental variables. In temperate regions (with severe winter), studies with birds have shown that temperature increases have led to larger clutch sizes (Jarvinen 1996; Przybylo et al. 2000; Møller 2002; Husek and Adamík 2008; Table 1). The mechanism involved in this physiological adjustment seems to be related to resource availability, since in these regions, the cold climate imposes food shortage (Jarvinen 1986, 1996) and higher temperatures lead to higher food availability, allowing species to have a higher number of broods. Annual variation in temperature, which reflects seasonality of resources, was the most important variable to explain clutch size in a global assessment (Jetz et al. 2008). For example, clutch size of owls in Finland is strongly determined by the abundance of rats: warmer years, with thinner snow cover, favour higher abundance of rats, allowing larger clutch size (Lehikoinen et al. 2011). Such positive relationship between food availability and mean clutch size in birds is well-known (Lack 1947; Price 1985; Gibbs and Grant 1987). Correlation between clutch size and climatic variables was also confirmed for other groups such as lizards (Smith et al. 1995; Abell 1999) and butterflies (Karlsson and Wiklund 2005; Saastamoinen 2007). In this sense, for species that live in temperate regions, where the cold is a limiting factor for population regulation, climate change may have positive impacts improving environmental conditions, increasing resource availability and allowing larger clutch size.

In the tropical region, resource seasonality is less intense and the reproductive season is longer, which allow species to attempt reproduction more frequently per season (Martin, 1996). A higher number of attempts to reproduce may lead to smaller clutch size, as the parents need to save energy to invest in the next clutch (Slagsvold 1984; Farnsworth

and Simons 2001). In the tropics, this seems to be a good strategy, since nest predation is higher than in the temperate region, which would allow the spread of predation risk in numerous reproduction attempts (Cody 1966; Kulesza 1990; Martin 1995; Griebeler et al. 2010; Table 1). If clutch size depends on nest predation rate, as proposed by Skutch (1949), that is, if larger broods attract more predators, then natural selection will favour smaller clutch sizes in the tropics (Martin et al. 2000). Considering that, a possible consequence of climate change to species that inhabit the tropics is that temperature increase and rainfall decrease might shorten the reproductive season, leading to a reduction in the number of reproduction attempts, which could force species to compensate by increasing clutch size (Lovette and Fitzpatrick 2016). That would represent a risk for species, since in the tropics nest predation rate is rather high, reaching 80-90% (revised by Stutchbury and Morton 2001).

In regions where climate change will cause temperature increase and significant rainfall decrease, making the areas more arid, species tend to reduce clutch size (Grant et al. 2000; Coe and Rotenberry 2003; Table 1). A study in the California desert has shown that, in territories that received water supplementation (treatment), a desert sparrow had significantly larger clutch size than in non-supplemented territories (control) (Coe and Rotenberry 2003). This result shows that environment variables not only have an indirect effect (regulating food availability) but might also act directly on physiology, so that supplemented females can allocate more water to egg production. During the reproductive period, females need a significantly higher amount of water to produce eggs, since they contain high percentage of water (Bartholomew and Cade 1963; Reynolds and Waldron 1999).

Another hypothesis used to explain smaller clutch size in the tropical region in comparison with the temperate region is known as egg-viability hypothesis (Stoleson and Beissinger 1999; Table 1). According to this hypothesis, in the tropics, where temperature is higher, extended exposure of the eggs to temperatures higher than 24-26°C (physiological zero) may trigger embryonic development even when the eggs are not being incubated. Such premature development of the embryos below optimum incubation temperature (36-38°C) results in abnormal growth of some tissues and consequent embryo death (Deeming and Ferguson 1992; Stoleson 1999). Therefore, birds that live in the tropics may lay smaller clutches so that they can start active incubation earlier in order to keep viability of the first eggs instead of waiting until many eggs are laid (Stoleson and Beissinger 1999). Based on this hypothesis, in a scenario of temperature increase, it is

expected that species initiate incubation earlier and earlier to avoid loss of the first eggs, which can lead to smaller clutch size, since premature incubation or contact with the eggs may interrupt follicular growth and egg laying (Haywood 1993).

Available evidence shows that species can adjust to climate change through phenotypic plasticity instead of altering their genetic constitution through microevolutionary adaptation (Gienapp et al. 2008). In general, there seems to be low or no additive genetic variation to clutch size and most intrapopulation variation is due to transitory environmental effects (Gibbs 1988). Species may present fast physiologic responses adjusting clutch size to environmental changes (Gibbs 1988; Baker 1995; Coe and Rotenberry 2003). For example, mean clutch size for sparrows in New York was 4.7 eggs, while in Costa Rica it was 2 eggs (reviews in Baker 1995). When sparrows captured in Costa Rica were raised in aviaries in New York, their clutch size was 3.50 ($\pm$ 0.46) eggs in the first year and 4.62 ($\pm$ 0.55) in the second year. Sparrows from New York raised in nearby aviaries under the same feeding conditions and same pressures had mean clutch size of 4.89 ($\pm$ 0.48) eggs (Baker 1995). This example shows that species do not need several generations to adjust their clutch size to climatic conditions. Therefore, negative impacts on species that will be forced to reduce their clutch size, such as low population recruitment, could occur in a rather accelerated pace, thus increasing their vulnerability.

Table 1. Possible mechanisms that explain how clutch size may influence species responses to climate change and their respective studies.

Pattern	Mechanism	Reference	Taxon	Location
In temperate regions, temperature increase may favour larger clutches	In cold regions, temperature increase leads to abundance of feeding resources	Jarvinen, 1996	Birds	Finland
		Przybylo et al., 2000	Birds	Sweden
		Moller, 2002	Birds	Denmark
		Husek and Adamik, 2008	Birds	Czech Republic
In the tropics, temperature increase and rainfall decrease may shorten reproductive season, decreasing the number of reproduction attempts and consequently reproductive success	In the tropics, reproductive season is longer and species may have more clutches with fewer eggs to spread predation risk, which is high.	Skutch, 1949	Birds	Central America
		Cody, 1966	Birds	Global
		Slagsvold, 1984	Birds	Norway
		Kulesza, 1990	Birds	Americas
		Martin, 1995	Birds	North America
		Martin, 2000	Birds	America
		Farnsworth and Simons, 2001	Birds	Theoretical model
Aridity may lead to reduction of clutch size	Lack of water may jeopardize egg production	Griebeler et al., 2010	Birds	Theoretical model
		Grant et al., 2000	Birds	Galápagos islands
In the tropics, temperature increase may reduce viability of the first eggs	Temperatures higher than 24-26°C induce embryonic development before incubation	Coe and Rotenberry, 2003	Birds	Mojave desert
		Deeming and Ferguson, 1992	Birds	Theoretical model
		Stoleson, 1999	Birds	Venezuela
		Stoleson and Beissinger, 1999	Birds	Venezuela

Diet breadth

In general, studies that assess climatic effects on diet are not focused on a specific taxon, but there is a prevalence of studies with vertebrates living in the temperate region (Table 2). Diet is an important trait that summarises distinct morphological, physiological and behavioural traits of a given organism, which determines how it interacts with the biotic and abiotic environments (Donnell et al. 2012; Abrahameczyk and Kessler 2014). It is expected that species with specialised diets present narrow niches, low local abundance and restricted geographic distribution (Mckinney 1997). On the other hand, generalist species have flexible behaviour and can change their feeding habits to adapt to changes in resource availability (O'Donoghue et al. 1998). Therefore, the diet breadth of a given species may influence its extinction risk (Boyles and Storm 2007). Species with a more specialised diet are associated with higher probabilities of negative response to climate change (Pacifici et al. 2017). We will discuss three main mechanisms species may respond to climate change through their diets (Table 2).

Climate change may affect the availability of feeding resources and in regions where these resources will decrease; species with specialised diets will become more sensitive, presenting higher extinction risk than generalist species (Chessman 2013). Species with broader diet breadth can avoid hunger by changing their diet to the available food item during adverse climatic conditions (Brändle et al. 2002). Such plasticity in diet is a mechanism that has allowed species to deal with climate-related fluctuations in availability and abundance of resources (Furness 1996; Ancona et al. 2012). Generalist species can increase diet diversity in response to unfavourable changes in the weather, when their preferred resources are scarce and they are led to supplement their diets with resources that are available at the moment (Folks et al. 2014; Gray et al. 2016; Table2). For example, temperature increase in North Pacific waters alters the availability of sea lion preys, making them change their diet, increasing the diversity of consumed preys (Robinson et al. 2018). In Northern Italy, owls have become more generalist under adverse climatic conditions (Rubolini et al. 2003). Alternatively, species with specialised diets may not be able to respond to resource fluctuation and therefore experience higher extinction risk. For mountain birds, temperature increase can result in population decrease caused by reduction in the abundance of preys, insects from Tipulidae family adapted to cold weather (Pearce-Higgins 2010). Temperature and rainfall increase during winter

caused significant decrease in Eastern quoll population due to reduction in the abundance of moth larvae (Fancourt et al. 2018).

Diet type may influence species ability to change their phenologic events (Altermatt 2010) and their distribution area (Angert et al. 2011) to follow climate change. Species that are not able to change their distribution areas fast enough to follow their adequate climatic conditions are under higher risk of extinction (Devictor et al. 2008), as well as those species that cannot change phenology to match species they interact with (Visser and Both 2005). Generally, diet generalists are expected to be more likely to find adequate resources in new areas, and should, therefore, present greater ability to change their distributions than specialists, which could be more limited by the phenology of species they depend on (Angert et al. 2011; Buckley and Kingsolver 2012). Broader diets can facilitate the expansion of distribution areas driven by climate (Braschler and Hill 2007) and the establishment and persistence of species in new environments (Estrada et al. 2016). However, a specialist may have greater probability of following spatial changes if its host species or prey also changes (Betzholtz et al. 2013; Auer and King 2014). Generally, diet specialists could be more affected by climate change since they present narrower distribution, are less likely to leave their habitats (Caldas 2014) and alter their phenologic events (Altermatt 2010) to track climatic conditions that are adequate.

Temperature increase may cause omnivore species to change their diet, becoming more herbivores and less carnivores (Table 2). For ectotherms, low body temperature makes herbivory energetically unfavourable, as it constrains the rate in which energy can be extracted from diet (Floeter et al. 2005; Boersma et al. 2016). For sea fish, herbivory is only possible above a threshold of 15°C (Floeter et al. 2005). There seems to be consensus on the fact that due to better digestion of vegetal material at high temperatures, ectotherms might maximise energy intake and maintain high metabolic rates in higher temperatures by increasing herbivory (Carreira et al. 2016). This idea is supported by studies that have found that herbivory increases in response to higher temperatures in several groups, such as Copepoda (Boersma et al. 2016), fish (Floeter et al. 2005), tadpoles (Carreira et al. 2016) and reptiles (Espinoza et al. 2004). Even amongst endotherms, herbivores tend to maintain higher body temperature than carnivores (Clarke and O'Connor 2014). Although omnivores can regulate their diet to deal with temperature increase caused by climate change, the ability to change to a more herbivore diet and its adaptive value is variable among species (Carreira et al. 2016). Besides, an increase in

herbivory in response to global warming can alter food chains, species interactions and the functioning of ecosystems.

Table 2. Possible mechanisms that explain how diet may influence species responses to climate change and their respective studies.

Pattern	Mechanism	Reference	Taxon	Location
Climate change may alter resource availability to species in the environment.	Generalists may increase the diversity of ingested items to include new options when their preferred resources are scarce	Folks et al. 2014	deer	Texas, USA
		Gray et al. 2016	marsupial	Australia
		Robinson et al. 2018	sea lion	California, USA
		Rubolini et al. 2003	owl	Northern Italy
		Bojarska and Selva 2012	brown bear	Holarctic
	There might be population decline when preferred food items are scarce	Pearce-Higgins et al. 2010	bird	United Kingdom
Climate change may force species to alter their phenology and distribution	Species with more flexible diets can change their phenology more easily to follow changes induced by the climate.	Altermatt 2010	Lepidoptera	Central Europe
		Braschler and Hill 2007	butterflies	Great Britain
	Generalist species can easily change their distribution areas following climate change	Angert et al. 2011	Passeriformes	North America
		Floeter et al. 2005	sea fish	Atlantic ocean
Alter omnivore diets	In higher temperatures, animals increase herbivory to maximize energy intake	Boersma et al. 2016	Copepoda	North Sea
		Carreira et al. 2016	tadpole	Iberian Peninsula
		Espinoza et al. 2004	reptile	South America
		Clarke and O'Connor 2014	bird and mammal	Global

Dispersal ability

Birds and lepidopterans are the best-represented taxa in studies regarding climatic effects on dispersal ability, and no studies were carried out in the tropical region (Table 3). Understanding species ability to respond to climate change is a fundamental point to identify species that experience higher risk (Møller et al. 2008; Hurlbert and Liang 2012). Species that are unable to change their annual cycles and their distributions to follow their suitable climatic conditions will be prone to higher extinction risk (Møller et al. 2008; Corlett and Westcott 2013). In this sense, dispersal ability is a crucial attribute for species and it is expected that those with higher dispersal ability respond more quickly to climate change, presenting lower extinction risk (Pöyry et al. 2009; Angert et al. 2011).

Climate change can affect the dispersal processes of organisms both directly and indirectly (Travis et al. 2013; Table 3). Indirect mechanisms (*eg.* altering resource availability and climatic suitability of the habitat) that may lead species to change their distribution areas and their annual cycles will be discussed in the next paragraphs (Table 3). On the other hand, climate change may directly interfere on behaviour, affecting the

organisms' decisions to stimulate or inhibit dispersal (Table 3). Higher temperatures increase dispersal of moths (Battisti et al. 2006), butterflies (Cormont et al. 2011) and birds (Møller et al. 2006) and decrease dispersal of lizards (Massot et al. 2008). Flooding increases dispersal of an aquatic bird in Canada (Roche et al. 2012) and the reduction of snow cover decreases dispersal of wolverines in the USA (Schwartz et al. 2009). These examples indicate that changes in climatic variables may increase or decrease dispersal depending on the system and the species (Travis et al. 2013). Moreover, species response may depend on the interaction of weather and landscape configuration (Delattre et al. 2013): in more fragmented landscapes, dispersal distance is longer at lower temperatures while in continuous landscapes, dispersal distance is longer at higher temperatures.

Recent climate change is quickly altering the location of areas that have suitable climate for certain species (Loarie et al. 2009), and, in order to survive, species must be able to move fast enough to follow such changes (Chen et al. 2011; Lenoir and Svenning 2015). Therefore, climate change as expected for the future might be a great threat to species persistence, since rates of distribution changes should be much higher than those observed in the past (Williams and Blois 2018). Some studies show that many organisms will not be able to disperse fast enough to follow their climatic niches, even highly mobile species (Pearson 2006; Devictor et al. 2008, 2012; Schloss et al. 2012). Species with low dispersal ability might lose significant parts of their distribution areas in the future (Krause et al. 2015), hence facing higher extinction risk (Pearson 2006; Corlett and Westcott 2013). Therefore, dispersal ability is a good predictor of species vulnerability to climate change. Both empirical observations (Warren et al. 2001; Hill et al. 2002; Pöyry et al. 2009; Angert et al. 2011) and model projections (Krause et al. 2015; Methorst et al. 2017; Williams and Blois 2018) evidence that higher dispersal ability indicates higher ability to change distribution to follow climate displacement (Table 3).

Recent global warming has already caused significant changes in many species' life cycles (Walther et al. 2002; Parmesan and Yohe 2003). Generally, plants and animals have advanced their phenologies in response to temperature increase (Parmesan and Yohe 2003; Parmesan 2006). However, consumers and predators at higher trophic levels in the food chain might not be able to respond in the same proportion, which can lead to a mismatch between reproductive period and resource availability (Visser et al. 1998, 2004; Visser and Both 2005). Species that cannot advance their arrival to reproduction sites to match the peak of food abundance may suffer population declines and, consequently, be more prone to extinction (Both et al. 2006; Møller et al. 2008).

Migratory birds should advance the beginning of migration to follow the phenology of plants and invertebrates in their reproduction areas (Sparks et al. 2005). Indeed, as a response to temperature increase in the last years, migratory birds have arrived earlier in their reproduction sites (Butler 2003; Hurlbert and Liang 2012). However, literature shows that long-distance migrants cannot respond to climatic change as quickly as short-distance migrants do, and arrive later (Table 3). This happens because long-distance migrants experience slower temperature increase in wintering areas in comparison to their reproduction areas, while short-distance migrants are exposed to warm weather throughout the year (Lehikoinen et al. 2004). Therefore, short-distance migrants have more and better cues to match their phenology with resource phenology (Jones and Cresswell 2010). Thus, long-distance migratory behaviour can represent an important constraint to responses to climate change, contributing to the decline of some species (Berthold et al. 1998; Møller et al. 2008; Jones and Cresswell 2010; Rubolini et al. 2010).

Table 3. Effects and possible mechanisms that explain how dispersal influences species responses to climate change and their respective studies.

Effect	Pattern	Mechanism	Reference	Taxon	Location
Direct	Affecting decision to disperse	Increasing/ stimulating dispersion	Battisti et al. 2006	Moths	Europe
			Cormont et al. 2011	Butterflies	Netherlands
			Roche et al. 2012	Aquatic birds	Canada
			Møller et al. 2006	Marine birds	Denmark
			Pärn et al. 2012	Sparrow	Norway
			Delattre et al. 2013	Butterflies	France
		Decreasing/ inhibiting dispersion	Schwartz et al. 2009	Wolverines	USA
			Massot et al. 2008	Lizzards	France
Indirect	Changing the distribution area	Higher dispersal ability, higher probability of tracking suitable environmental conditions	Bullock et al. 2012	Plants	Great Britain
			Pöyry et al. 2009	Butterflies	Finland
			Angert et al. 2011	Apine plants	Switzerland
			Hill et al. 2002	Butterflies	Great Britain
			Warren et al. 2001	Butterflies	Great Britain
			Krause et al. 2015	Plants	USA
			Methorst et al. 2017	Birds	Paleartic
			Williams and Blois 2018	Mammals	North America
	Changing phenological responses	Short-distance migrants respond more quickly to climate change than long-distance migrants.	Butler 2003	Birds	North America
			Swanson and Palmer 2009	Birds	USA
			Tryjanowski et al. 2002	Birds	Poland
			Tøttrup et al. 2010	Birds	Europe
			Hurlbert and Liang 2012	Birds	North America
			Rubolini et al. 2010	Birds	Germany
			Végvári et al. 2010	Birds	Europe
			Rubolini et al. 2007	Birds	Europe
			Thorup et al. 2007	Birds	Europe

Climatic tolerance

Studies assessing species climatic tolerance are focused on ectotherms and most of them were carried out on a global scale (Table 4). Tolerance to climatic conditions is one of the most important factors that determine how species are distributed around the globe (Thomas 2010). Variation on climatic tolerance among species is an important characteristic to determine their responses to climate change, as it is able to alter distribution and survival (Deutsch et al. 2008; Huey et al. 2012; Caldwell et al. 2015; Rugiu et al. 2018). Species with higher thermic tolerance occupy broader geographic areas (Bozinovic et al. 2011) and will be able to deal better with global warming (Calosi et al. 2008; Buckley et al. 2012; Huey et al. 2012). In general, the thermic tolerance of an organism is proportional to the magnitude of temperature variation experienced in its habitat, steeply increasing with latitude (Deutsch et al. 2008). Thus, species from the tropics, which inhabit environments with lower temperature variation throughout the year, have narrower thermic tolerance than species from temperate regions (Deutsch et al. 2008; Huey et al. 2009, 2012; Duarte et al. 2012; Khaliq et al. 2014; Table 4). Deutsch et al. (2008) have reported that heat tolerance in tropical insects is, on average, only one fifth of the tolerance of insect species from temperate regions. Besides that, tropical species already live in warmer environments, close to their critical temperature, in comparison with species from temperate regions, which live in colder environments, far from their critical temperature (Sunday et al. 2012; Araújo et al. 2013; Khaliq et al. 2014). Therefore, even small temperature increases might be a threat to tropical species.

Heat tolerance is more conserved amongst lineages than cold tolerance, implying that many species might have lost their evolutionary potential to respond to global warming (Addo-Bediako et al. 2000; Huey et al. 2009; Araújo et al. 2013). When organisms are exposed to temperatures close to their upper thermal limit, biological activity suffers from several limitations and might compromise survival (Somero 2011). Furthermore, it is unlikely that species are able to persist under conditions that surpass their limits of physiological tolerance (Calosi et al. 2010). Thus, climatic conditions expected in the future might negatively affect population abundance and potentially compromise their persistence (Rugiu et al. 2018). However, while tropical species might be severely affected, species from temperate regions might benefit from temperature increase, responding with higher rates of population growth and aptitude (Deutsch et al. 2008; Caldwell et al. 2015; Carrascal et al. 2016; Table 4).

Such pattern of greater physiological vulnerability to climatic changes in tropical species, when compared to species from temperate areas, has been shown to ectotherms, especially reptiles (Deutsch et al. 2008; Tewksbury et al. 2008; Huey et al. 2009, 2010; Diamond et al. 2012; Duarte et al. 2012; Sunday et al. 2012; Hoffmann et al. 2013; Caldwell et al. 2015). For endotherms, on the other hand, the relationship between higher thermic tolerance in species that experience higher climatic variability was observed in birds but not in mammals (Khaliq et al. 2014). Even though most ectotherms, particularly those from the temperate region, might tolerate projected temperature increases across significant ranges of their distributions, potential vulnerability to projected temperatures increases from polar regions to tropical areas (Khaliq et al. 2014). Unlike the observed pattern for ectotherms (Addo-Bediako et al. 2000; Deutsch et al. 2008), endotherms present low phylogenetic conservatism regarding climatic tolerance, so they can respond to temperature increase through physiological adaptation (Khaliq et al. 2015). In temperate regions, endotherms distribution is limited by extremes of low temperature, via physiological cold tolerance of species (Khaliq et al. 2017), so that scenarios of global warming might benefit species living in those regions, increasing their abundance (Carrascal et al. 2016). In the tropics, endotherms (especially mammals) seem to be limited by other factors, such as biotic interactions, rather than climatic conditions (Khaliq et al. 2017).

Overall, species that present the lowest climatic tolerances will be more affected by climate change, so that species from the tropical region and mainly ectotherms will be more vulnerable to projected temperature increases in the future (Table 4). Endotherms can keep high and constant body temperature, which is in general independent from the direct influence of ambient climatic conditions (MacNab 2012). On the other hand, ectotherms might be more vulnerable as their physiology, locomotion, growth and reproduction are strongly influenced by ambient temperature (Deutsch et al. 2008). Moreover, warmer temperatures may force ectotherms to spend more time in shelters to avoid lethally high temperatures, restricting the time available for other important activities such as foraging, territory defence and mating (Sinervo et al. 2010). Due to their low ability to respond to climate change, several ectotherm populations were locally extinct in recent decades and temperature increase might lead to extinction of almost 40% of lizard populations and 20% of lizard species globally until 2080 (Sinervo et al. 2010).

Table 4. Possible mechanisms that explain how climatic tolerance may influence species responses to climate change and their respective studies.

Pattern	Mechanisms	Reference	Taxon	Location
Species from tropical regions are more vulnerable to climatic change than species from temperate regions	Species from tropical regions have narrower thermic tolerance and live in environments where the temperature is close to their upper thermal limit	Deutsch et al. 2008	ectotherms	global
		Tewksbury et al. 2008	ectotherms	global
		Huey et al. 2009	lizards	neotropics
		Sunday et al. 2012	ectotherms	global
		Huey et al. 2012	ectotherms	global
		Diamond et al. 2012	ants	global
		Hoffmann et al. 2013	ectotherms	global
		Khaliq et al. 2014	endotherms	global
		Caldwell et al. 2015	lizards	Tasmania
Species from temperate regions are less vulnerable and may benefit from climate change	Species present broader thermic tolerance and live in environments where the temperature is far from their upper limits	Deutsch et al. 2008	ectotherms	global
		Sunday et al. 2012	ectotherms	global
		Huey et al. 2012	ectotherms	global
		Khaliq et al. 2014	endotherms	global
		Caldwell et al. 2015	lizards	Tasmania
		Carrascal et al. 2016	birds	Spain
Ectotherms are more vulnerable to climate change than endotherms	Ectotherms present higher niche conservatism and lower capacity adjust their physiology	Addo-Bediako et al. 2000	insects	global
		Deutsch et al. 2008	ectotherms	global
		Sinervo et al. 2010	lizards	Mexico
		Khaliq et al. 2015	birds and mammals	global
		Khaliq et al. 2017	birds and mammals	global

Conclusions

Overall, the literature review performed regarding the four chosen traits enabled us to present and discuss some mechanisms that might explain species responses to climate change. As shown here, response to climate change is highly variable among species and regions. Some species may exhibit a critical response to a specific climate variable, while others may have a minimal response and some might even present a contradictory response from what is expected, depending on the region they inhabit. Explaining such variation has become a great challenge to conservationists in this century. Such explanation would allow the identification of species at higher extinction risk, the definition of the best conservation strategies and the strategic direction of resources. It was also possible to verify bias concerning region and taxa in the evaluated studies. The tropical region, which holds more sensitive species, was weakly represented, while most studies have focused on the temperate region. For some traits, studies concentrate on a specific group and neglect others, for example, most studies assessing climatic tolerance have focused on reptiles.

Species that are exposed to higher magnitude of climate warming should present more pronounced biological responses (Chen et al. 2011). However, intrinsic differences between species' life history traits, physiology and other ecological characteristics are fundamental to determine their vulnerability (Williams et al. 2008; Foden et al. 2013).

Assessments of climate change vulnerability that consider both exposure and traits that determine sensitivity and adaptive ability could be useful tools (Foden et al. 2013; Böhm et al. 2016). However, trait choice should be based on empirical evidence that shows the relevance of such traits in determining the vulnerability of assessed species.

In this review, we show that the four evaluated traits are important predictors of species responses to climate change and we present the main mechanisms involved in each response. Therefore, clutch size, diet breadth, dispersal ability and climatic tolerance are important traits to be considered in vulnerability assessments. Even though some evidence might lead us to conclude that species with smaller clutch size, with specialised diets, low dispersal ability and lower climatic tolerance would experience higher risk due to climate change, the set of studies evaluated here indicates that the risk depends on the region and the species group considered. While species from the temperate region could benefit from temperature increase with greater resource availability, increasing clutch size and expanding the distribution area through dispersal, species from the tropics could be severely affected as they have lower climatic tolerance and already live close to their limits of heat tolerance. Vulnerability is higher for ectotherms, because, unlike endotherms, they cannot control body temperature and their biological activities depend on the climatic conditions of the environment. Apparently, ectotherms from the tropical region will not be able to escape from temperature increase through dispersal (Buckley et al. 2013).

It is possible that the lack of response in a trait interferes in the response of another trait. In the temperate region, temperature increase causes advanced flowering in plants and abundance of insects. Thus, birds that spend the winter in other regions should be able to advance their arrival so that the reproductive period matches the period of food availability. Species that cannot advance their arrival might face food scarcity during reproduction, which can lead to smaller clutch size. In the tropics, species present lower thermic tolerance and this might affect their dispersal ability to follow suitable climatic conditions if they have to cross warmer areas.

As we understand the mechanisms involved in the response of other traits, we will be able to enhance our ability to predict climate change impacts, enabling conservation practices that are more adequate to protect species. The increase of this type of studies could facilitate the understanding of which characteristics are more informative to each species group within each region. Besides that, understanding the mechanisms through which traits influence species responses to climatic changes may help justify the traits

included in vulnerability assessments, improving their results and making them more useful. For that, CCVAs need to be more integrated with the ecology literature that aims to assess how species traits respond to changes in the climate.

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Bird vulnerability to climate and land use changes in the Brazilian Cerrado

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Abstract

Estimating species vulnerability to global changes and understanding what drives their vulnerability has become an important task in the last decades. Here, we evaluated the vulnerability of Cerrado bird species to climate and land use changes projected to take place up to 2050, compared our vulnerability estimates to the national red list of threatened species, and evaluated the level of protection of vulnerable species. For 103 species we gathered information on biological traits and associated them to three components of vulnerability (sensitivity, adaptive capacity and exposure). For each trait, we assigned high or low scores according to their relationship with climate and land use changes. We considered as exposed, sensitive and with low adaptive capacity those species that reached a high score in any of the traits. Species that reached a high score for all the three components were classified as highly vulnerable. We found that 67%, 71% and 39% of species were sensitive, had low adaptive capacity or were exposed, respectively; 25% of them were highly vulnerable. Among these species, 10 are currently threatened in Brazil. Overall, the network of protected areas (PAs) harbors a small extent of highly vulnerable species' range, with 19 species (73%) having <10% of range coverage within PAs. Understanding which species are the most vulnerable and where they are found is crucial to establish conservation priorities aiming to mitigate the negative impacts of environmental changes on species.

Keywords: Adaptation, Climate change vulnerability assessments, Diversity patterns, Extinction risk, Protected areas, Tropical savanna

Introduction

Climate and land use changes are main threats to biodiversity. Consequences of these threats are reflected in decreasing abundance, fitness and population genetic variability, phenological changes, changes in trophic interaction, range shifts and, ultimately, extinction (Fahrig, 2003; Parmesan, 2006). However, owing to their intrinsic traits and adaptation capabilities, species respond to these environmental changes in different ways (Foden et al., 2013; Maggini et al., 2014).

Vulnerability is defined as the predisposition to being negatively affected (IPCC, 2014), and can be assessed based on three components: sensitivity, adaptive capacity and exposure to a harmful event. Sensitivity lies is the ability to withstand climate change and is generally related to life-history traits such as physiological tolerance and degree of habitat specialization. Adaptive capacity refers to a species ability to deal with climate change, either by adapting to new local conditions or by moving to more suitable areas. Exposure, on the other hand, is determined by the rate and magnitude of changes in climate and species habitat (Dawson et al., 2011; Foden et al., 2013). An effective assessment of environmental change threats to biodiversity requires the identification of highly vulnerable species as well as the drivers of such vulnerability.

Climate Change Vulnerability Assessments (CCVAs) is an analytical framework that has been increasingly used for defining priorities for biodiversity conservation and management (Foden et al., 2013; Carr et al., 2014; Bohm et al., 2016; Foden et al., 2019). This framework assesses a species' relative vulnerability by using biological traits to estimate species sensitivity, adaptive capacity and exposure to climate change. Climate Change Vulnerability Assessments retrieve scores of species relative vulnerability (Pacifci et al., 2015; Foden and Young, 2016). Currently, several CCVAs has been done. However, nearly 88% of these studies considered only exposure in their assessments (see Thompson et al., 2015). Further, South America stands out as the least investigated region in CCVAs (Pacifci et al., 2015). Here, we used a trait-based approach that accounts for species sensitivity, adaptive capacity and exposure to climate and land use changes.

Birds may be particularly impacted by environmental changes. Changes in land use can eliminate their habitats leading up to local extinctions, besides triggering indirect impacts such as increased predation and nest parasitism (Borges and Marini, 2010). In some regions, the beginning of bird breeding season is dependent on the beginning of the rainy season (Marini et al., 2012). Reproductive success may be also affected by

precipitation and temperature, indirectly mediated by higher rates of predation during warmest and driest periods (Borgman and Wolf, 2016). Higher temperatures lead to increased body temperature, metabolism and water loss through perspiration, and the costs of these activities may affect bird survival and fitness (McKechnie and Wolf, 2010; Cunningham et al., 2013). Worldwide, climate change associated with habitat loss might lead to the extinction of hundreds of bird species (Şekercioğlu et al., 2008).

Here, we evaluated the relative vulnerability of birds inhabiting the Brazilian Cerrado by adopting a trait-based approach that accounts for species sensitivity, adaptive capacity and exposure to projected climate and land use changes. Beyond climate change, we also consider land use change as an exposure factor. Specifically, we will: 1) identify highly vulnerable species in relation to land use and climate changes; 2) highlight the main traits associated with species' relative vulnerability; 3) compare the results of our vulnerability assessment with extinction risk classification of Brazil's threatened species; 4) map the spatial patterns related to the different components of vulnerability, and 5) assess the representativeness of highly-vulnerable species in the network of protected areas of the Brazilian Cerrado.

Methods

Study region and species

The Cerrado is a South American biogeographical province located in an area of high future climatic instability and high degradation of natural vegetation, which may harbor a high number of species vulnerable to environmental change (Watson et al., 2013; Strassburg et al., 2017). Climate forecasts for the Cerrado point towards a temperature increase of 5 to 5.5 °C and a decrease in the precipitation regimen ranging from 35 to 45% (PBMC, 2013). Around 31 to 34% of the remaining native Cerrado vegetation may be eliminated by 2050 mostly due to the low protection and the high pressure exerted by agriculture expansion (Soares-Filho et al., 2016; Strassburg et al., 2017; Vieira et al., 2018). Besides, protected areas cover 8.3% of the Cerrado, only 3% of which are considered integral protection (Francoso et al., 2015).

The Cerrado harbors 856 bird species (Silva, 1995; Silva and Santos, 2005), 30 of which are endemic (Silva and Bates, 2002) and 32 threatened to extinction according to the Brazil's Red Book on Threatened Species (ICMBio, 2018). Cerrado bird species feature highly distinct geographical patterns, ranging from endemic species with

restricted distribution such as *Asthenes luizae*, to cosmopolitan ones, such as *Pandion haliaetus*.

We selected a sample of 856 Cerrado bird species for the following reasons: 1) the focus of our study are bird species widely distributed across the Cerrado, excluding those occurring only marginally and 2) as the land use model that we used to calculate species exposure covers only the Brazilian territory, we chose to include in the analysis only those Cerrado species that have at least 90% of their distribution within Brazil, which lead to a selection of a subset of 103 bird species. Range maps of these species were retrieved from BirdLife International (<http://www.birdlife.org/datazone/info/spcdownload>). These maps have yielded matrices of presence/absence of species through the overlapping of such maps in a grid of approximately 9×9 km (5 min latitude/longitude). Any given species was considered present in the cell when its distribution overlapped 50% or more of the cell.

Climate data

Bioclimatic variables for the current (1960–1990) and future (2050) time periods were retrieved from the WorldClim database (version 1.4; www.worldclim.org/version1) (Hijmans et al., 2005). For the future scenario, we used climate projections from 15 Atmosphere-Ocean General Circulation Models (AOGCMs: ACCESS1-0, BCC-CSM1-1, CCSM4, CNRM-CM5, GISS-E2-R, HadGEM2-AO, HadGEM2-CC, HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM-CHEM, MIROC-ESM, MIROC5, MPI-ESM-LR, MRI-CGCM3 e NorESM1-M) in a scenario of high greenhouse gas emissions (RCP 8.5, IPCC, 2013). This seems to be the most likely scenario given the trends for greenhouse gas emissions since the year 2000 and, besides, only minor differences have been noticed across all RCPs until 2050 (Diffenbaugh and Field, 2013; IPCC, 2013).

To avert collinearity issues among the 19 bioclimatic variables, we carried out a factorial analysis to choose those that explain the highest variation in the data (Terribile et al., 2012). The selected bioclimatic variables to quantify bird species exposure were: 1) Mean Diurnal Range of Temperature (BIO2); 2) Temperature Seasonality (BIO4); 3) Mean Temperature of Warmest Quarter (BIO10); 4) Precipitation of Wettest Quarter (BIO16) and 5) Precipitation of Driest Quarter (BIO17). The bioclimatic variables for the current and future scenarios were obtained in a resolution of approximately 9×9 km (5 min latitude/ longitude).

Trait selection and thresholds

One of the limitations of trait-based vulnerability assessments is the lack of available traits for species' assessments as well as the uncertainty related to the thresholds used to define the highest risk of extinction (Pacifiçi et al., 2015; Foden et al., 2019). Here, we used traits for which we find available data. For the categorically assessed traits, the thresholds were defined in a clearer and objective way: species that occupy only one habitat type, that migrate and are rare were considered as “high” sensible, while the others were considered with “low” sensitivity. For fecundity, since only three species have average clutch size lower than two eggs (Table S1), we considered the species that lay up to two eggs with “low” adaptive capacity, and those that lay more than two eggs with “high” adaptive capacity (this trait ranged from 1 to 7.5 eggs per clutch). However, this threshold is subjective, and does not necessarily represent a real threshold. For the traits of adaptability (dispersal ability and climate tolerance), we selected a threshold of 25% of the species with the lowest values, as considered them as having “low” adaptability, while the others were considered as with “high” adaptability. We adopted the same threshold of 25% of the highest values to classify the species that are most exposed to climate and land use changes. Species with the highest values were considered as “highly exposed”, while the others were considered as “less exposed”. Although these thresholds are arbitrary, they provide an easy approach to categorizing a continuous variable into a binary risk of extinction (high or low). This approach is also commonly used and accepted in similar vulnerability assessments (Foden et al., 2013, Carr et al., 2014, Bohm et al., 2016).

Sensitivity

Species sensitivity to climate change was determined based on information on the three traits listed below. The thresholds and the number of classified species within the high and low sensitivity categories for each trait are described in Table 1.

Habitat specialization

Species presenting high degree of specialization tend to be the most sensitive to environmental changes than generalist species with wider geographical range (Cardillo et al., 2005). Sensitivity may be higher when the habitat in which the species has specialized is particularly vulnerable to the impacts of environmental change. We quantified habitat specialization according to the number of different habitats (from 1 to 5) where the

species is found based on the classification proposed by Parker III et al. (1996). Species associated to a single habitat received a high sensitivity score.

Migratory status

Migratory species are generally considered more sensitive to environmental changes than their non-migrating counterparts, since they must adjust their movements to climatic conditions that foster breeding and survival in different environments (Both et al., 2010). We classified species as migratory and non-migratory according to Somenzari et al. (2018). Species that perform any type of migration were assigned high sensitivity scores.

Rarity

Rare species may be more negatively affected by environmental changes than common and abundant species, as they are usually more vulnerable to catastrophic events, present low genetic variability and low recovery capacity. We ranked rarity according to the relative species abundance according to Parker III et al. (1996), who classify species as common (1), fairly common (2), uncommon (3) and rare (4). Moreover, species within each of these four categories may also present an uneven aggregated distribution. In these cases, species were penalized in 0.5 point. For example, uncommon species that present aggregated distribution received a score of 3.5. Species that scored 3.5 or more were considered highly sensitive.

Adaptability

We assessed the adaptive capacity of each species based on three traits: dispersal ability, climatic breadth and fecundity. The threshold and the number of species classified as having high and low adaptability for each trait are summarized in Table 1.

Dispersal ability

Species that present low dispersal ability will probably present lower ability to respond to environmental changes, since they will not be able to move fast enough to keep up with suitable climate conditions. Since dispersal ability is difficult to be measured and data for this trait are not available, we used an alteration of Kipp's index as proposed by Claramunt et al. (2012) as a surrogate for species dispersal ability. This index is based on two measurements of birds' wings. The first one is wing length, from the carpal joint

until the distal extremity of the longest primary feather, and the second one is secondary length, from the carpal joint until the distal extremity of the longest secondary feather. Evidence from literature shows this index is a good indicator of dispersal ability in birds (Baldwin et al., 2010; Dawideit et al., 2009). High values of the index indicate higher dispersal ability. Wing measurements for the 103-studied species were carried out in museum specimens from the Museu de Zoologia from the Universidade de Sao Paulo and in the Colecao Ornitologica Marcelo Bagno from the Universidade de Brasilia. Measurements were taken from the closed right wing using a digital caliper or a tape measure (for large specimens). Whenever possible, we measured three males and three females of each species, collected from different regions, to obtain a mean value for the species. This is important because, besides sexual dimorphism, several species also present significant morphological differences due to geographic variation (Lopes and Gonzaga, 2014). Species presenting the 25% lowest values for Kipp's index were assigned low adaptability scores.

Climatic tolerance

Species that can occupy areas with higher climate ranges will probably have higher ability to adapt to environmental changes, since they present higher phenotypic plasticity or higher genetic diversity (Brown, 1995). We used annual mean temperature, obtained from the monthly means between 1960 and 1990, to quantify each species' climatic breadth (bioclimatic variable BIO1 in WorldClim). This variable, as well as the aforementioned ones, was obtained at a 5-minute (latitude/ longitude degree) resolution. After that, we determined the range (maximum – minimum value) within the distribution areas of each species. Species presenting the 25% lowest values were assigned low adaptability scores.

Fecundity

Species that present low fecundity are usually associated with high extinction risk (Lee and Jetz, 2011). On the other hand, species that present high fecundity rates are more capable of colonizing habitats and adapting to environmental changes (Duncan et al., 2001). Since fecundity data are limited, we used mean clutch size (number of eggs) as a surrogate for species fecundity. We gathered data for this trait from different sources (Sick, 1997; del Hoyo et al., 2012 and from the website www.wikiaves.com.br). There was no information available regarding brood size for nine species (8.8%). In those cases,

we inferred the values from the closest congeneric species. Species with average clutch size of up to two eggs were assigned low adaptability scores.

Exposure

We used two measurements to quantify exposure: climate exposure and land-use exposure. The threshold and the number of species assigned high and low exposure for each variable are summarized in Table 1.

We assessed climate exposure by quantifying the proportion of the species distribution area in which climate conditions in 2050 will exceed the current climate range experienced by the species (1960–1990). We used current climate conditions for each one of the five aforementioned bioclimatic variables to determine the range (maximum – minimum) to which each species is currently exposed to within their distribution. In each cell of the grid, we calculated the mean and standard deviation for projections obtained with the 15 AOGCMs for the five bioclimatic variables. To estimate the value of each bioclimatic variable in 2050, we subtracted one standard deviation from the mean of each of the 15 AOGCMs. We then quantified the proportion of the species distribution area in which climate conditions in 2050 will exceed the climate conditions currently experienced by the species (see B.R. Ribeiro et al., 2016, V. Ribeiro et al., 2016). Species presenting the 25% highest proportions were assigned high climate exposure scores.

To quantify exposure to land-use changes, we used the maps produced by Soares-Filho et al. (2016) for the periods of 2012 and 2050 at 500m resolution. This spatially explicit model simulates land-use changes and associated carbon emissions under different scenarios regarding deforestation and demands for agricultural land in Brazil (for more details, see Soares-Filho et al., 2016). We considered as suitable habitats for each species only those cells presenting native vegetation (areas used for agriculture, livestock and urbanization were not included). To assess the exposure to land-use changes, we calculated the proportion of native vegetation within each species distribution area for the two periods. We considered as “exposed” cells that were occupied by native vegetation in 2012 but will have been converted to other uses by 2050. Species presenting the 25% highest exposure proportions were assigned high land-use exposure scores.

Vulnerability

We determined species vulnerability to environmental changes according to the methodology proposed by IUCN (Foden et al., 2013; Carr et al., 2014), which assesses the three components of vulnerability: sensitivity, adaptability and exposure. According to this method, the most vulnerable species are those that present high sensitivity, high exposure and low adaptability (represented by the overlapping area between the three components in Fig. 1).

We assigned high or low scores for the different traits considered in each component of vulnerability. All species assigned high scores for any of the traits within each component of vulnerability were considered sensitive species, presenting low adaptability and being exposed to environmental changes (Table 1; Foden et al., 2013). For example, any given species was considered sensitive if it was assigned a high habitat specialization score, even though it received low scores for the other two traits of the sensitivity component. We classified species as highly vulnerable to environmental changes only if they received high scores for all three components (sensitivity, adaptability and exposure). This approach was also used and is well established by other authors (Foden et al., 2013; Carr et al., 2014; Bohm et al., 2016). We also compared species that are most vulnerable to environmental changes with those listed as endangered (Critically endangered - CR, Endangered - EN and Vulnerable - VU categories) in the list of threatened species in Brazil.

We are aware of the new approach presented in the IPCC's Fifth Assessment Report (IPCC, 2014). Instead of considering “vulnerability” as a general measure of concern, the new approach considers “risk”. Risk is defined as the likelihood of harmful consequences resulting from climate change, arising from the interaction between vulnerability, exposure and hazard (IPCC, 2014). Then, vulnerability and exposure are the intrinsic factors and the hazard is the extrinsic factor (see Foden et al., 2019 for further details on the differences between the two approaches). Although the structure of the new approach is useful in many ways, we have chosen to use the previous approach presented by the IPCC's Fourth Report because it was widely adopted by the conservation community, is better aligned with our objectives and data. Further, this new approach still received little attention in the literature, and we do not know how well supported it would be (see also Foden et al., 2019).

Spatial analyses

In order to examine spatial distribution of the different components of vulnerability to environmental changes (Fig. 1) we divided the study area in a grid composed of cells of approximately 9×9 km. We stacked each species distribution map to this grid to calculate species richness in each cell. Species were considered present in a cell if it overlapped any part of their distribution area. We constructed richness maps of the following groups: exposed species, sensitive species, species with low adaptability, species that are most vulnerable (intersection between the three components) and species listed as threatened (CR, EN and VU categories) by the Brazilian national red list.

Vulnerable species and protected areas

We obtained spatial data regarding Protected Areas (PAs) from the National System of PAs (CNUC) made available by the Brazilian Ministry of Environment (MMA, <http://www.mma.gov.br/areasprotegidas/cadastro-nacional-de-ucs>). There are 1638 registered PAs in Brazil, encompassing the National, State and Municipality administration. To verify whether species that were considered more vulnerable to environmental changes are represented within PAs, we overlapped species distribution areas and PA distribution in Brazil. Although Brazilian PAs have different management categories, in this study we did not evaluate these categories separately. However, we verified and corrected spatial overlap among PAs and kept those individually mapped. We then calculated the proportion of each species distribution that occurs inside all PAs in Brazil according to our grid. A cell was considered protected if any part of it overlapped a given PA.

Table 1. Traits used to assess (under sensitivity, adaptability and exposure) the vulnerability of the 103 bird species to environmental changes, including trait description, thresholds and number of species classified in high and low vulnerability categories.

Traits/Variables	Description	Thresholds	Low	High
<i>Sensitivity</i>				
Habitat specialization	Number of habitats a species occurs in.	Low: > 1 High: = 1	69	34
Migratory status	Migratory or non-migratory.	Low: resident High: migrant	96	7
Rarity	Relative species abundance in the environment.	Low: < 3.5 points High: ≥ 3.5 points	77	26
<i>Adaptability</i>				
Dispersal ability	Species Kipp's index.	Low: 75% highest High: 25% lowest	77	26
Climatic tolerance	Temperature breadth (maximum – minimum) within species range.	Low: 75% highest High: 25% lowest	77	26
Fecundity	Species clutch size.	Low: > 2 eggs High: ≤ 2 eggs	51	52
<i>Exposure</i>				
Climatic exposure	Proportion of species range that will be exposed to climatic variations by 2050 above or below current values.	Low: 75% lowest High: 25% highest	77	26
Land-use exposure	Proportion of species range that will lose native vegetation by 2050.	Low: 75% lowest High: 25% highest	77	26

Results

Sensitivity

We classified 50 species (48.5%) as sensitive to environmental changes. Habitat specialization was the most important trait defining species sensitivity (for 33 species), followed by abundance (for 26 species) and migratory status (for 7 species). *Sporophila bouvreuil* was the only species sensitive according to all traits. Fourteen species were sensitive according to two traits, and 35 species (34%) were considered highly sensitive owing to a single trait (Table S1).

Adaptability

We found 73 species (71%) with low adaptability to environmental changes. Regarding this vulnerability component, low fecundity was the main trait responsible for low adaptability (n=52), followed by dispersal ability (n=26), and width of climatic niche (n=26). Six species had low adaptability regarding all three analyzed traits, while 48 species had low adaptability owing to a single trait (Table S1). Climatic tolerance varied

from 1.1°C to 26.6°C. Species with the lowest and highest climatic tolerance were *Synallaxis simoni* and *Hirundinea bellicosa*, respectively. According to the Kipp's index, *Taoniscus nanus* and *Penelope ochrogaster* showed the lowest dispersal ability, while the hummingbirds *Lophornis magnificus* and *Heliactin bilophus* presented the highest values for the index. Only seven species had clutch size of four or more eggs (Table S1).

Exposure

Forty species (39%) showed high values of exposure to environmental changes by 2050. Since our threshold corresponds to the 25% highest values for exposure, the same number of species (n=26) were exposed due to climate change and to land-use change (Table 1). Among those 40 species, 13 were exposed to climate and land use changes simultaneously, 13 were exposed to climate only and 14 were exposed to land-use change only (Table S1). Further, temperature of the warmest quarter and precipitation of the driest quarter contributed most to species exposure (Table S2).

Seven species were also exposed to climate variables in >85% of their distribution areas, and three of them (*Cercomacra ferdinandi*, *Conothraupis mesoleuca* and *Synallaxis simoni*) had 100% exposure (Table S1). *Paroaria baeri* had the highest exposure to land-use change, followed by *Celeus obrieni*, with exposure proportions of 28.3% and 20.6% respectively.

Vulnerability and threat

We classified 22 species (21%, out of 103 studied species) as highly vulnerable to environmental changes (*i.e.* combining sensitivity, low adaptability and exposure, Fig. 1). We found four species (4%) to be likely exposed and sensitive (but with high adaptability, a.k.a. potential adapters), ten species (10%) with high exposure and low adaptive capacity (but not sensitive, a.k.a. potential persisters) and 17 species (16%) as having high sensitivity and low adaptive capacity (but not likely exposed, *i.e.* species with high latent risk). From the 103 assessed species, 15 (14.6%) figure on the list of Brazilian threatened species (being two species classified as CR, eight species as EN, and five species as VU). Ten of the 22 highly-vulnerable species are also threatened with extinction, according to the national list.

Geographical patterns of vulnerability and protected areas

Species with high sensitivity and low adaptability followed the overall species richness pattern of the study species, being concentrated in the south and central region of the Cerrado (Fig. 2). Species that are highly exposed were concentrated in the northwestern region. While we found highly vulnerable species distributed across all the Cerrado, threatened species were south (Fig. 2). All 22 highly-vulnerable species had a relatively low proportion of their distributions occurring inside PAs. Only two species (*Cercomacra ferdinandi* and *Nyctiprogne vielliardi*) had >25% of its distribution inside PAs, while 15 species (68.2%) had <10%. The most extreme case was registered to *Pyrrhura pfrimeri*, which fell completely out of Pas (Table 2).

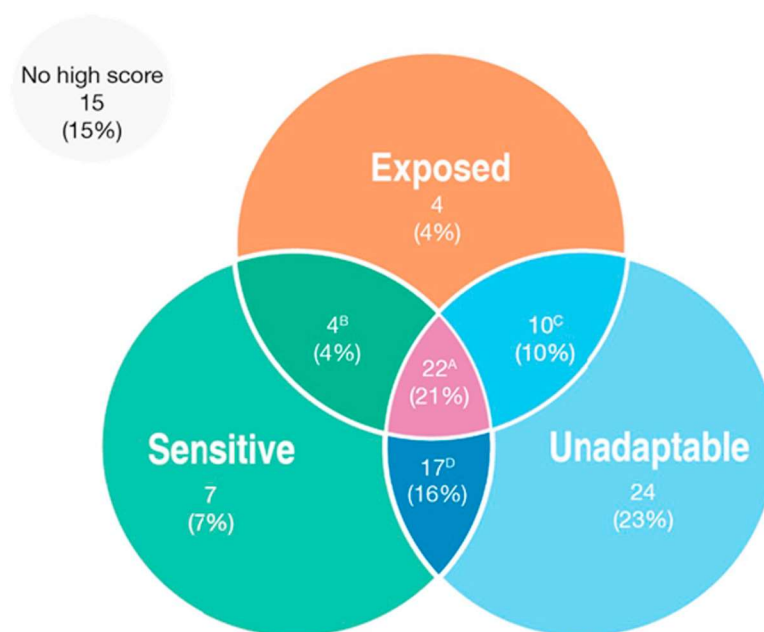


Figure 1. The three dimensions of species vulnerability to environmental changes and their combinations. A: highly vulnerable species (intersection between the three dimensions). These are the species with greatest concern; B: potential adapters (exposed and sensitive, but highly adapted species); C: potential persisters (exposed and poorly adapted, but not sensitive species); D: high latent risk (sensitive species with low adaptation, but not exposed yet).

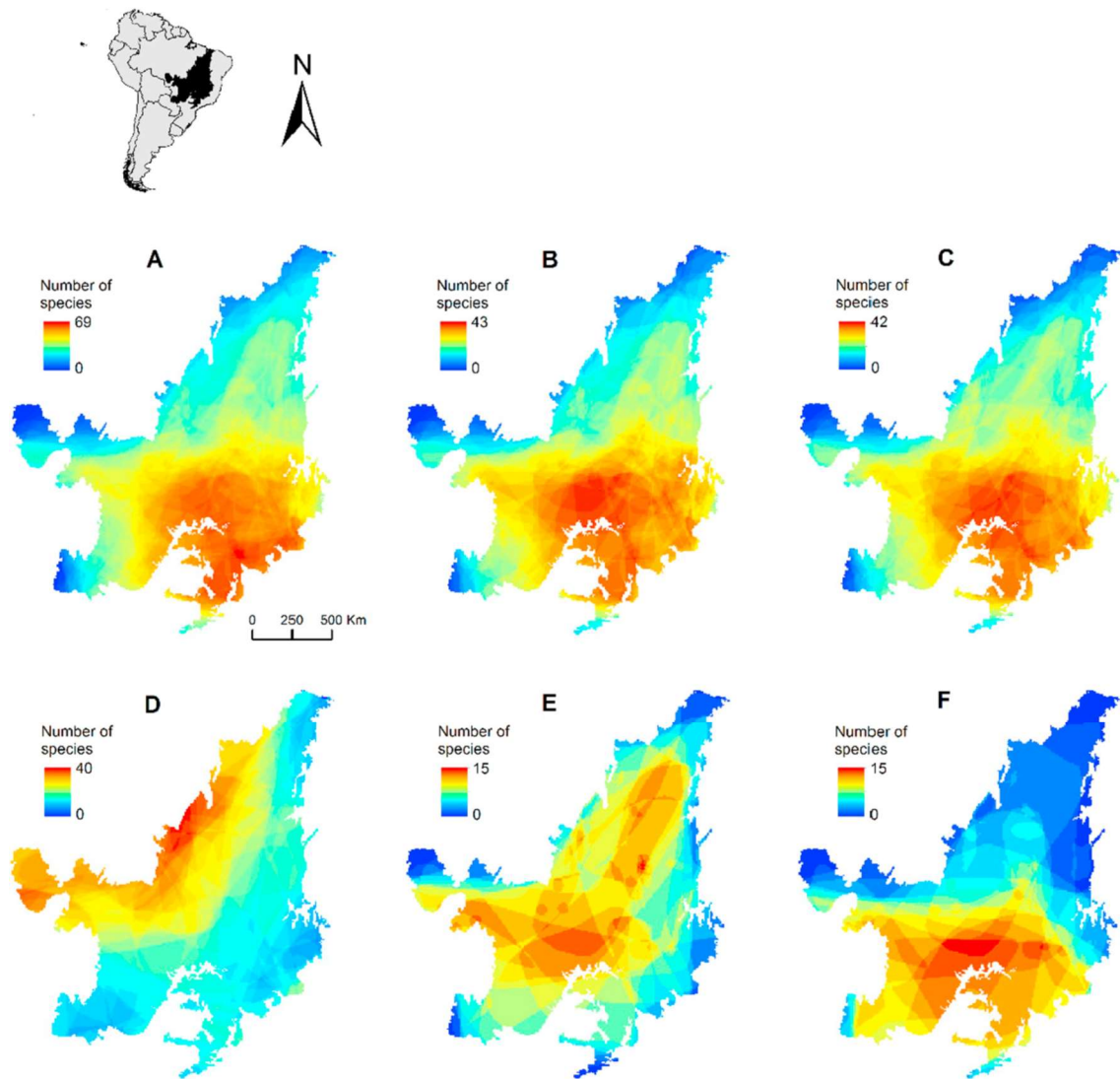


Figure 2. Patterns of species richness for the different groups of bird species that occur in the Brazilian Cerrado. A: overall pattern for all 103 species evaluated; B: species sensitive to environmental changes (n=50); C: species with low adaptability to environmental changes (n=73); D: species exposed to environmental changes (n=40); E: most vulnerable species to environmental changes (n=22); F: species found in the list of threatened species in Brazil (n=15).

Table 2. Proportion of the distribution area of the 22 species most vulnerable to environmental changes occurring within Protected Areas (PAs).

Species	Range proportion inside PAs (%)
<i>Anodorhynchus hyacinthinus</i>	14
<i>Antilophia galeata</i>	5.6
<i>Aratinga jandaya</i>	9.8
<i>Attila phoenicurus</i>	18.6
<i>Celeus obrieni</i>	8.3
<i>Cercomacra ferdinandi</i>	30
<i>Charitospiza eucosma</i>	7.1
<i>Columbina cyanopis</i>	2.1
<i>Conothraupis mesoleuca</i>	3.8
<i>Euscarthmus rufomarginatus</i>	6.7
<i>Herpsilochmus longirostris</i>	6.8
<i>Knipolegus franciscanus</i>	10.2
<i>Nyctiprogne vielliardi</i>	27.7
<i>Penelope ochrogaster</i>	10
<i>Phaethornis nattereri</i>	6.7
<i>Phyllomyias reiseri</i>	8.8
<i>Phylloscartes roquettei</i>	6.2
<i>Porphyrospiza caerulescens</i>	6.8
<i>Pyrrhura pfrimeri</i> ^a	0
<i>Scytalopus novacapitalis</i>	6.2
<i>Sporophila melanogaster</i>	6.4
<i>Uropelia campestris</i>	10

^a Records for *P. pfrimeri* do exist in one PA (Parque Estadual Terra Ronca; Miller et al., 2013), but BirdLife data do not capture such occurrences.

Discussion

We identified the Brazilian Cerrado bird species that are highly vulnerable to environmental changes, as well as the drivers of their vulnerability. Further, we highlighted the regions where different components of vulnerability concentrate, compared the geographic distribution of highly-vulnerable species with that of threatened ones and estimated the proportion of highly-vulnerable species distribution that occurs within protected areas.

We found variation in species vulnerability. Understanding the causes of such variation and identifying species that will probably be more and less vulnerable are important steps to the development of adaptation strategies and to the establishment of

priorities for conservation actions against the negative impacts associated with environmental changes (Garnett et al., 2013; Carr et al., 2014). For each one of the four distinct classes of species vulnerability different conservation strategies have been suggested (Foden et al., 2013). The 22 highly-vulnerable species should have their responses to environmental changes monitored with priority and interventions will be likely necessary. Potential adapters might be capable of dispersing to regions that are more suitable or adapting to climate change through microevolution. However, close monitoring of their populations is necessary to verify whether these responses are taking place. Regarding potential persisters, population trends should be monitored to verify whether they can cope with climate change *in situ*. Lastly, species with high latent risk should have their habitats monitored, since they could become vulnerable to environmental changes if they come to be exposed after the period analyzed here (see also Foden et al., 2013).

Temperature of the warmest quarter and precipitation of the driest quarter were the climatic variables responsible for exposing the highest number of species to future climate change expected by 2050 (Table S2). Climate change might strongly affect bird species distribution in the Cerrado (B.R. Ribeiro et al., 2016, V. Ribeiro et al., 2016), as extreme temperatures are likely a limiting factor to bird distribution, so that species with narrower temperature breadth could be more affected than those with wider breadth (Jiguet et al., 2006). Species that inhabit tropical regions are particularly vulnerable to climate change since they already experiment temperature conditions close to their tolerance limits (Araujo et al., 2013; Khaliq et al., 2014), besides, they have low ability of physiological adaptation and reduced plasticity (Hoffmann et al., 2013; Araujo et al., 2013). Changes in rainfall regime might affect species reproduction, since the onset of bird breeding season is directly related to the onset of the rainy season (Santos and Marini, 2010; Duca and Marini, 2011; Marini et al., 2012). Most bird species have a short breeding season of three months (from September to November), which corresponds to the period of highest abundance of food resources (Marini et al., 2012). A possible imbalance between resource demand and availability might reduce bird reproductive success (Both et al., 2006; Saino et al., 2011).

Six species (*Cercomacra ferdinandi*, *Conothraupis mesoleuca*, *Nyctiprogne vielliardi*, *Paroaria baeri*, *Pyrrhura pfrimeri* and *Synallaxis simoni*) would be likely exposed to climate change in nearly all their current distribution areas by 2050. All of them present restricted distribution ranges, four of them are endemic to the Cerrado (C.

ferdinandi, *P. baeri*, *P. pfrimeri* and *S. simoni*) and three of them are threatened (*C. ferdinandi*, *C. mesoleuca* and *P. pfrimeri*). *Cercomacra ferdinandi* and *S. simoni* occur only in Araguaia river basin and are highly dependent on the river-created habitats (Silva, 1997; Olmos et al., 2006). These restrictions lead to extreme vulnerability regarding these two species. Among the 22 species identified as highly vulnerable to environmental changes, ten (*Anodorhynchus hyacinthinus*, *Celeus obrieni*, *Cercomacra ferdinandi*, *Columbina cyanopis*, *Conothraupis mesoleuca*, *Penelope ochrogaster*, *Phylloscartes roquettei*, *Pyrrhura pfrimeri*, *Scytalopus novacapitalis* and *Sporophila melanogaster*) are listed as threatened in Brazil. The remaining 12 species (54.5%), which are not threatened according to the Brazilian list but were considered vulnerable in our study, should receive special attention to determine the extent to which environmental changes impacts could interfere with their probability of extinction (Carr et al., 2014).

The potential consequences of the extinction of most vulnerable species to ecosystems should not be neglected. *Antilophia galeata*, for instance, is an abundant bird in the gallery forests of the Cerrado, where it is an important seed disperser of small-sized fruits (Marini, 1992), including several plant species important to the process of ecological succession. *Penelope ochrogaster*, as the several cracid species, is a disperser of large-sized seeds, providing unique ecological services (Delacour et al., 2004). *Phaethornis nattereri* is a hummingbird that probably adopt a trapliner strategy as its congeners, like *P. pretrei*, which is acknowledge as a keystone species in the Cerrado (Araujo et al., 2018). Additionally, the most charismatic among those vulnerable species, such as *Anodorhynchus hyacinthinus* and *Pyrrhura pfrimeri*, are also important flagship species. Their extinction could hamper ongoing conservation efforts, such as those prompted by the recent rediscovery of the Critically Endangered *Columbina cyanopis* after 75 years since its last confirmed record, which resulted in the creation of the Botumirim State Park, with ca. 36,000 ha (www.savebrasil.org.br/rolinha-do-planalto-pebotumirim/).

The list of threatened species in Brazil follows the same methods of the IUCN Red List. Even though they are part of IUCN Red List criteria, future threats related to climate and land-use changes are rarely considered in the assessment of species threat status. Further, it is known that the Red List is not completely effective in considering climate change impact (Akçakaya et al., 2006). Assessments of vulnerability to environmental changes, such as the one presented in this study, are useful to identify species that are not currently threatened but will probably become in the future, so that

this information can be used to complement endangered species lists (Bagne et al., 2014; Maggini et al., 2014; Meng et al., 2016). >60% of species that are vulnerable to climate change are not listed as threatened in Brazil. However, species that are common nowadays might present rapid declines under specific circumstances (Gaston and Fuller, 2007) and are not necessarily immune to extinction nor resistant to environmental changes (Bagne et al., 2014).

Low spatial congruence on the distribution of species classified into different vulnerability components is usually found (Foden et al., 2013; Lee et al., 2015), and suggest that different aspects of vulnerability might be important in different locations. Due to likely exposure to high temperatures in northwestern Cerrado, many species will likely have to disperse to other areas. Studies assessing the climate change effects on the Cerrado fauna have shown that areas with more suitable future climate for birds (Marini et al., 2009a), non-flying mammals (Loyola et al., 2012; Faleiro et al., 2013) and bats (Aguilar et al., 2016) will be in south Cerrado. However, this region is the most developed and highly populated region, so that around 85% of native vegetation has been already replaced, mainly by pasture and crops (Sano et al., 2010). Even if species can disperse to areas with more suitable climate in the future, their survival and permanence in those areas might be strongly affected by the lack of adequate habitats (see Loyola et al., 2012). Further, nearly 68% of species that are vulnerable to climate change had <10% of their current distributions represented in PAs. Marini et al. (2009b) has shown that PAs in the Cerrado are currently inefficient to ensure bird conservation, and such inefficiency tends to increase in the future due to climate change. Thus, to ensure higher efficiency of PAs we should consider long-term planning, including dynamic factors such as climate and land-use changes (Monteiro et al., 2018).

Because of the high rates of climate and land use changes predicted for this century, conservation managers need to make informed decisions and vulnerability assessments are important tools to guide these decisions. Here, we pointed out species that will likely be most vulnerable and the regions they occur for more intensive monitoring. We highlight important aspects of vulnerability, such as the traits of life history that can increase sensitivity and decrease the adaptive capacity of species in face of environmental changes.

Considering our results, some actions have proven to be necessary to ensure long-term permanence of species. First, it is necessary to monitor populations of the most vulnerable species to verify how they will react to environmental changes. Second, it is

necessary to implement ecological corridors connecting the northern and southern regions to allow exposed species occurring in the North or Northwest to disperse to the south, tracking climatic conditions that are more suitable, with lower exposure. Third, since the species that were considered threatened by the Brazilian list are concentrated in the southern region, which is highly fragmented and presents low native vegetation cover, it is necessary to create new protected areas and encourage the recovery of degraded areas, increasing the size and connectivity of native vegetation reminiscent. We believe that these actions can help reduce the species' vulnerability to the environmental changes expected in the coming decades.

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Supplementary Material

Table S2. Number of species that may be exposed by 2050 to each of the five bioclimatic variables selected.

Bioclimatic variables	Number of species exposed
Mean Diurnal Range (BIO2)	03
Temperature Seasonality (BIO4)	11
Mean Temperature of Warmest Quarter (BIO10)	103
Precipitation of Wettest Quarter (BIO16)	0
Precipitation of Driest Quarter (BIO17)	49

Table S1. Traits and their respective scores used to estimate the vulnerability of Cerrado bird species to environmental changes within each of the three dimensions, including threat categories for those present on Brazil's endangered species list. For more details on each trait see the Methods section.

Species	Sensitivity							Adaptative capacity						Exposure					Threatened in Brazil		
	Habitats number	Score habitats	Migratory status	Score migratory	Abundan ce	Score abundanc	Sensitive	Dispers al	Score dispersal	Climatic breadth	Score climatic	Fecundity	Score Fecund.	Low Adaptabili	Climatic exposure	Score climatic	Land-use exposure	Score land-use		Exposed	
Alipiopsitta xanthops	2	LOW	breeding res	LOW		3	LOW	NO	2.3	LOW	9.6	HIGH	3	LOW	YES	29.5	LOW	17.3	HIGH	YES	NO
Amazilia lactea	3	LOW	breeding res	LOW		2	LOW	NO	6.0	LOW	14.0	LOW	2	HIGH	YES	19.5	LOW	5.2	LOW	NO	NO
Anodorhynchus hyacinthinus	5	LOW	breeding res	LOW		4	HIGH	YES	2.0	LOW	7.4	HIGH	2.5	LOW	YES	49.6	HIGH	13.4	LOW	YES	EN
Antilophia galeata	1	HIGH	breeding res	LOW		2	LOW	YES	1.1	HIGH	12.4	LOW	2	HIGH	YES	33.4	LOW	14.6	HIGH	YES	NO
Aphantochroa cirrochloris	2	LOW	breeding res	HIGH		3	HIGH	YES	6.3	LOW	13.3	LOW	2	HIGH	YES	7.9	LOW	4.5	LOW	NO	NO
Aratinga auricapillus	2	LOW	breeding res	LOW		4	HIGH	YES	3.1	LOW	12.9	LOW	3	LOW	NO	26.2	LOW	3.9	LOW	NO	NO
Aratinga jandaya	3	LOW	breeding res	LOW		4	HIGH	YES	3.4	LOW	7.5	HIGH	3	LOW	YES	47.5	HIGH	18.2	HIGH	YES	NO
Asemospiza fuliginosa	5	LOW	nomadic	LOW		3.5	HIGH	YES	1.4	LOW	17.4	LOW	2.5	LOW	NO	11.1	LOW	2.7	LOW	NO	NO
Asthenes luizae	1	HIGH	breeding res	LOW		3	LOW	YES	1.3	LOW	6.4	HIGH	3	LOW	YES	11.2	LOW	4.1	LOW	NO	NO
Attila phoenicurus	2	LOW	transient shr	HIGH		3.5	HIGH	YES	2.0	LOW	15.1	LOW	2	HIGH	YES	43.8	HIGH	5.6	LOW	YES	NO
Augastes scutatus	1	HIGH	breeding res	LOW		2	LOW	YES	6.2	LOW	6.6	HIGH	2	HIGH	YES	18.5	LOW	2.6	LOW	NO	NO
Automolus leucophthalmus	1	HIGH	breeding res	LOW		2	LOW	YES	1.5	LOW	13.4	LOW	3.5	LOW	NO	26.0	LOW	4.5	LOW	NO	NO
Baryphthengus ruficapillus	3	LOW	breeding res	LOW		1	LOW	NO	0.7	HIGH	12.3	LOW	2.5	LOW	YES	22.1	LOW	3.3	LOW	NO	NO
Casiornis fuscus	1	HIGH	breeding shr	HIGH		2	LOW	YES	1.4	LOW	9.7	LOW	2.5	LOW	NO	41.7	HIGH	16.3	HIGH	YES	NO
Celeus flavescens	4	LOW	breeding res	LOW		2	LOW	NO	1.0	HIGH	15.0	LOW	2.8	LOW	YES	21.3	LOW	11.3	LOW	NO	NO
Celeus obrieni	1	HIGH	breeding res	LOW		4	HIGH	YES	0.9	HIGH	7.3	HIGH	2.5	LOW	YES	50.4	HIGH	20.6	HIGH	YES	VU
Celeus ochraceus	4	LOW	breeding res	LOW		2	LOW	NO	1.2	LOW	14.1	LOW	2.8	LOW	NO	34.7	LOW	9.0	LOW	NO	NO
Cercomacra ferdinandi	1	HIGH	breeding res	LOW		2	LOW	YES	1.0	HIGH	2.3	HIGH	2	HIGH	YES	100.0	HIGH	10.6	LOW	YES	VU
Charitospiza eucosma	1	HIGH	breeding res	LOW		3.5	HIGH	YES	1.4	LOW	22.9	LOW	2	HIGH	YES	23.9	LOW	14.5	HIGH	YES	NO
Clibanornis rectirostris	1	HIGH	breeding res	LOW		4	HIGH	YES	1.0	HIGH	9.8	LOW	2.5	LOW	YES	16.6	LOW	8.6	LOW	NO	NO
Columbina cyanopis	1	HIGH	breeding res	LOW		4	HIGH	YES	0.9	HIGH	5.8	HIGH	2	HIGH	YES	39.9	HIGH	10.6	LOW	YES	CR
Compsothraupis loricata	2	LOW	breeding res	LOW		3	LOW	YES	2.1	LOW	9.7	LOW	2.5	LOW	NO	28.3	LOW	15.8	HIGH	YES	NO
Conopophaga lineata	3	LOW	breeding res	LOW		1	LOW	YES	0.8	HIGH	13.0	LOW	2	HIGH	YES	26.7	LOW	5.2	LOW	NO	NO
Conothraupis mesoleuca	1	HIGH	breeding res	LOW		4	HIGH	YES	1.7	LOW	2.7	HIGH	2.5	LOW	YES	100.0	HIGH	19.3	HIGH	YES	EN
Cranioleuca semicinerea	1	HIGH	breeding res	LOW		3	LOW	YES	1.5	LOW	9.7	LOW	2.5	LOW	NO	22.0	LOW	13.0	LOW	NO	NO
Cyanocorax cristatellus	1	HIGH	breeding res	LOW		2	LOW	YES	1.3	LOW	15.0	LOW	5.7	LOW	NO	33.0	LOW	14.1	HIGH	YES	NO
Cyanocorax cyanopogon	2	LOW	breeding res	LOW		2	LOW	NO	0.7	HIGH	15.2	LOW	4	LOW	YES	26.3	LOW	14.1	HIGH	YES	NO
Cypseloides senex	3	LOW	breeding res	LOW		2.5	LOW	YES	6.3	LOW	11.5	LOW	1	HIGH	YES	28.6	LOW	9.0	LOW	NO	NO
Cypsnagra hirundinacea	2	LOW	breeding res	LOW		2.5	LOW	NO	1.6	LOW	13.9	LOW	2.8	LOW	NO	26.5	LOW	15.0	HIGH	YES	NO
Dendrocolaptes platyrostris	3	LOW	breeding res	LOW		2	LOW	NO	1.7	LOW	15.0	LOW	3.4	LOW	NO	14.1	LOW	10.5	LOW	NO	NO
Diopsittaca cumanensis	2	LOW	breeding res	LOW		2	LOW	NO	3.3	LOW	15.2	LOW	4	LOW	NO	21.4	LOW	12.5	LOW	NO	NO
Elaenia sordida	5	LOW	breeding res	LOW		3	LOW	NO	1.8	LOW	13.1	LOW	2	HIGH	YES	27.5	LOW	5.9	LOW	NO	NO
Embernagra longicauda	1	HIGH	breeding res	LOW		3	LOW	YES	1.4	LOW	7.1	HIGH	2	HIGH	YES	11.5	LOW	3.7	LOW	NO	NO
Eupetomena macroura	3	LOW	breeding res	LOW		2	LOW	NO	6.3	LOW	15.2	LOW	2	HIGH	YES	24.2	LOW	10.9	LOW	NO	NO
Eupsittula cactorum	1	HIGH	breeding res	LOW		2	LOW	YES	3.2	LOW	9.7	LOW	6	LOW	NO	29.2	LOW	13.5	HIGH	YES	NO
Euscarthmus rufomarginatus	2	LOW	breeding res	LOW		4.5	HIGH	YES	1.2	LOW	10.1	LOW	2	HIGH	YES	38.3	HIGH	13.6	HIGH	YES	NO
Fluvicola nengeta	2	LOW	breeding res	LOW		2	LOW	YES	1.6	LOW	15.2	LOW	2.5	LOW	NO	19.7	LOW	9.9	LOW	NO	NO
Formicivora melanogaster	1	HIGH	breeding res	LOW		2	LOW	YES	0.9	HIGH	11.4	LOW	2	HIGH	YES	20.7	LOW	12.7	LOW	NO	NO
Furnarius figulus	3	LOW	breeding res	LOW		2	LOW	YES	0.6	HIGH	15.2	LOW	2	HIGH	YES	25.2	LOW	11.3	LOW	NO	NO
Geositta poeciloptera	1	HIGH	breeding res	LOW		3.5	HIGH	YES	1.0	HIGH	12.4	LOW	2.9	LOW	YES	24.7	LOW	9.9	LOW	NO	EN
Heliactin bilophus	2	LOW	breeding res	LOW		3	LOW	NO	6.7	LOW	15.0	LOW	2	HIGH	YES	23.0	LOW	12.1	LOW	NO	NO
Heliomaster squamosus	4	LOW	breeding res	LOW		3.5	HIGH	YES	6.2	LOW	13.5	LOW	2	HIGH	YES	5.8	LOW	8.9	LOW	NO	NO
Hemithraupis ruficapilla	3	LOW	breeding res	LOW		1	LOW	NO	1.9	LOW	12.1	LOW	2.5	LOW	NO	14.7	LOW	1.6	LOW	NO	NO
Herpsilochmus atricapillus	2	LOW	breeding res	LOW		1	LOW	YES	1.2	LOW	12.7	LOW	2	HIGH	YES	27.4	LOW	13.2	LOW	NO	NO
Herpsilochmus longirostris	1	HIGH	breeding res	LOW		2	LOW	YES	1.0	HIGH	10.3	LOW	2	HIGH	YES	35.5	HIGH	14.6	HIGH	YES	NO
Hirundinea bellicosa	3	LOW	breeding res	LOW		2.5	LOW	YES	3.3	LOW	26.6	LOW	2	HIGH	YES	25.6	LOW	12.3	LOW	NO	NO
Hylophilus amaurocephalus	5	LOW	breeding res	LOW		1	LOW	NO	1.0	HIGH	13.2	LOW	2	HIGH	YES	12.8	LOW	9.8	LOW	NO	NO
Icterus jamacaii	1	HIGH	breeding res	LOW		1	LOW	YES	1.6	LOW	9.7	LOW	2.5	LOW	NO	31.5	LOW	15.3	HIGH	YES	NO
Ilicura militaris	2	LOW	breeding res	LOW		2	LOW	NO	1.9	LOW	12.0	LOW	2	HIGH	YES	12.8	LOW	2.2	LOW	NO	NO
Knipolegus franciscanus	1	HIGH	breeding res	LOW		3	LOW	YES	1.9	LOW	5.8	HIGH	3	LOW	YES	41.3	HIGH	7.7	LOW	YES	NO

Knipolegus lophotes	2 LOW	breeding res LOW	2 LOW	NO	2.7 LOW	14.0 LOW	3 LOW	NO	23.1 LOW	9.3 LOW	NO	NO
Knipolegus nigerrimus	3 LOW	breeding res LOW	3 LOW	YES	1.9 LOW	15.0 LOW	3 LOW	NO	2.9 LOW	6.3 LOW	NO	NO
Lepidocolaptes squamatus	2 LOW	breeding res LOW	2 LOW	YES	2.1 LOW	12.9 LOW	2 HIGH	YES	18.3 LOW	4.4 LOW	NO	NO
Lophornis magnificus	2 LOW	breeding res LOW	3 LOW	NO	6.6 LOW	14.9 LOW	2 HIGH	YES	15.8 LOW	8.5 LOW	NO	NO
Melanerpes flavifrons	2 LOW	breeding res LOW	2 LOW	NO	2.6 LOW	13.2 LOW	2.5 LOW	NO	23.7 LOW	3.0 LOW	NO	NO
Melanopareia torquata	2 LOW	breeding res LOW	2.5 LOW	YES	0.7 HIGH	12.4 LOW	2 HIGH	YES	26.1 LOW	14.7 HIGH	YES	NO
Mergus octosetaceus	2 LOW	breeding res LOW	4 HIGH	YES	3.2 LOW	13.7 LOW	7.5 LOW	NO	24.1 LOW	5.3 LOW	NO	CR
Microspingus cinereus	1 HIGH	breeding res LOW	4 HIGH	YES	1.4 LOW	9.7 LOW	3 LOW	NO	26.1 LOW	11.0 LOW	NO	NO
Myiothlypis leucophrys	1 HIGH	breeding res LOW	3 LOW	YES	1.6 LOW	10.4 LOW	2 HIGH	YES	32.0 LOW	11.1 LOW	NO	NO
Neopelma pallescens	3 LOW	breeding res LOW	2.5 LOW	NO	1.7 LOW	12.8 LOW	1.8 HIGH	YES	29.7 LOW	13.7 HIGH	YES	NO
Neothraupis fasciata	1 HIGH	breeding res LOW	2 LOW	YES	1.0 HIGH	12.3 LOW	3 LOW	YES	19.8 LOW	12.8 LOW	NO	NO
Nothura minor	1 HIGH	breeding res LOW	4 HIGH	YES	1.1 HIGH	8.8 HIGH	4 LOW	YES	25.2 LOW	7.7 LOW	NO	EN
Nyctiprogne vielliardi	1 HIGH	breeding res LOW	4.5 HIGH	YES	3.7 LOW	3.8 HIGH	2 HIGH	YES	97.3 HIGH	11.8 LOW	YES	NO
Paroaria baeri	2 LOW	breeding res LOW	2 LOW	NO	1.2 LOW	5.5 HIGH	2 HIGH	YES	97.0 HIGH	28.3 HIGH	YES	NO
Paroaria dominicana	2 LOW	breeding res LOW	1 LOW	NO	1.3 LOW	9.7 LOW	3 LOW	NO	26.1 LOW	12.3 LOW	NO	NO
Penelope ochrogaster	1 HIGH	breeding res LOW	3 LOW	YES	0.4 HIGH	5.6 HIGH	2 HIGH	YES	87.1 HIGH	18.6 HIGH	YES	VU
Penelope superciliaris	2 LOW	breeding res LOW	2 LOW	NO	1.2 LOW	15.2 LOW	2.4 LOW	NO	25.5 LOW	10.6 LOW	NO	NO
Phaethornis nattereri	1 HIGH	breeding res LOW	2 LOW	YES	5.8 LOW	6.8 HIGH	2 HIGH	YES	45.3 HIGH	18.6 HIGH	YES	NO
Phyllomyias fasciatus	3 LOW	breeding res LOW	3.5 HIGH	YES	1.7 LOW	15.2 LOW	2 HIGH	YES	14.2 LOW	9.9 LOW	NO	NO
Phyllomyias reiseri	2 LOW	breeding res LOW	3.5 HIGH	YES	1.9 LOW	6.3 HIGH	2 HIGH	YES	46.4 HIGH	15.3 HIGH	YES	NO
Phylloscartes roquettei	1 HIGH	breeding res LOW	3.5 HIGH	YES	3.6 LOW	6.9 HIGH	2.4 LOW	YES	46.5 HIGH	8.1 LOW	YES	EN
Poecilotriccus fumifrons	3 LOW	breeding res LOW	2 LOW	YES	1.2 LOW	7.1 HIGH	2.5 LOW	YES	67.4 HIGH	9.3 LOW	YES	NO
Polystictus superciliaris	1 HIGH	breeding res LOW	3 LOW	YES	1.5 LOW	12.9 LOW	2 HIGH	YES	4.3 LOW	3.9 LOW	NO	NO
Porphyropsiza caerulescens	1 HIGH	breeding res LOW	3.5 HIGH	YES	1.0 HIGH	9.6 HIGH	2 HIGH	YES	14.2 LOW	15.3 HIGH	YES	NO
Primolius maracana	2 LOW	breeding res LOW	4 HIGH	YES	3.0 LOW	15.0 LOW	2 HIGH	YES	26.5 LOW	10.5 LOW	NO	NO
Pteroglossus inscriptus	3 LOW	breeding res LOW	2 LOW	NO	1.2 LOW	7.1 HIGH	2.8 LOW	YES	42.4 HIGH	10.3 LOW	YES	NO
Pyrrhura pflimeri	1 HIGH	breeding res LOW	2 LOW	YES	2.9 LOW	3.9 HIGH	5 LOW	YES	98.3 HIGH	17.3 HIGH	YES	EN
Saltator atricollis	2 LOW	breeding res LOW	2.5 LOW	NO	1.0 HIGH	14.9 LOW	2.5 LOW	YES	21.9 LOW	12.9 LOW	NO	NO
Schiffornis virescens	3 LOW	breeding res LOW	2 LOW	NO	1.2 LOW	12.4 LOW	2 HIGH	YES	29.7 LOW	3.9 LOW	NO	NO
Schistochlamys ruficapillus	4 LOW	breeding res LOW	2 LOW	NO	1.1 LOW	14.9 LOW	2.5 LOW	NO	24.7 LOW	10.3 LOW	NO	NO
Sclerurus scansor	2 LOW	breeding res LOW	3 LOW	YES	1.4 LOW	13.9 LOW	2.5 LOW	NO	19.8 LOW	6.3 LOW	NO	NO
Scytalopus novacapitalis	1 HIGH	breeding res LOW	4 HIGH	YES	1.1 HIGH	5.9 HIGH	2 HIGH	YES	65.6 HIGH	8.9 LOW	YES	EN
Sirystes sibilator	2 LOW	breeding res LOW	2.5 LOW	NO	1.8 LOW	15.1 LOW	2.5 LOW	NO	37.0 HIGH	6.4 LOW	YES	NO
Sporophila albogularis	3 LOW	breeding res LOW	2 LOW	NO	1.4 LOW	9.7 LOW	2 HIGH	YES	25.4 LOW	11.8 LOW	NO	NO
Sporophila bouvreuil	1 HIGH	breeding res HIGH	3.5 HIGH	YES	1.3 LOW	15.2 LOW	2 HIGH	YES	27.4 LOW	12.5 LOW	NO	NO
Sporophila cinnamomea	3 LOW	wintering sh HIGH	3 LOW	YES	1.5 LOW	11.6 LOW	2 HIGH	YES	33.7 LOW	13.1 LOW	NO	NO
Sporophila melanogaster	2 LOW	wintering sh HIGH	3 LOW	YES	1.5 LOW	12.7 LOW	2 HIGH	YES	35.8 HIGH	5.3 LOW	YES	VU
Sporophila palustris	3 LOW	wintering sh HIGH	2.5 LOW	YES	1.2 LOW	11.5 LOW	2 HIGH	YES	28.3 LOW	12.5 LOW	NO	VU
Streptoprocne biscutata	5 LOW	breeding res LOW	2.5 LOW	YES	6.4 LOW	15.2 LOW	1.7 HIGH	YES	10.4 LOW	7.0 LOW	NO	NO
Suiriri affinis	2 LOW	breeding res LOW	2 LOW	NO	1.8 LOW	9.6 LOW	2 HIGH	YES	39.7 HIGH	17.4 HIGH	YES	NO
Synallaxis scutata	2 LOW	breeding res LOW	3 LOW	YES	0.9 HIGH	22.1 LOW	2.5 LOW	NO	26.4 LOW	14.7 HIGH	YES	NO
Synallaxis simoni	2 LOW	breeding res LOW	1 LOW	YES	0.9 HIGH	1.1 HIGH	3 LOW	YES	100.0 HIGH	12.4 LOW	YES	NO
Syndactyla dimidiata	2 LOW	breeding res LOW	3 LOW	YES	1.8 LOW	13.5 LOW	2.5 LOW	NO	25.6 LOW	10.8 LOW	NO	NO
Tachyphonus coronatus	3 LOW	breeding res LOW	1 LOW	NO	1.5 LOW	13.3 LOW	2.5 LOW	NO	5.8 LOW	3.3 LOW	NO	NO
Tangara flava	5 LOW	breeding res LOW	2 LOW	NO	1.8 LOW	15.2 LOW	2 HIGH	YES	21.3 LOW	12.5 LOW	NO	NO
Taoniscus nanus	2 LOW	breeding res LOW	3 LOW	NO	0.4 HIGH	8.8 HIGH	3 LOW	YES	22.1 LOW	7.9 LOW	NO	EN
Thalurania glaucopsis	3 LOW	breeding res LOW	1 LOW	NO	6.2 LOW	13.2 LOW	2 HIGH	YES	3.4 LOW	3.9 LOW	NO	NO
Thamnophilus pelzelni	1 HIGH	breeding res LOW	1 LOW	YES	1.0 HIGH	9.7 LOW	2 HIGH	YES	23.2 LOW	13.5 HIGH	YES	NO
Thamnophilus torquatus	3 LOW	breeding res LOW	2 LOW	YES	1.1 HIGH	15.0 LOW	2 HIGH	YES	22.4 LOW	12.8 LOW	NO	NO
Turdus subalaris	3 LOW	breeding sh HIGH	2 LOW	YES	2.3 LOW	14.4 LOW	3 LOW	NO	26.2 LOW	9.6 LOW	NO	NO
Uropelia campestris	2 LOW	breeding res LOW	3.5 HIGH	YES	1.0 HIGH	8.3 HIGH	2 HIGH	YES	47.0 HIGH	18.2 HIGH	YES	NO
Xiphocolaptes albicollis	3 LOW	breeding res LOW	3 LOW	NO	1.2 LOW	13.4 LOW	2 HIGH	YES	24.1 LOW	5.0 LOW	NO	NO
Xiphorhynchus fuscus	2 LOW	breeding res LOW	2 LOW	YES	1.9 LOW	14.2 LOW	2.5 LOW	NO	6.6 LOW	3.8 LOW	NO	NO

Climate and land-use change refugia for Brazilian Cerrado birds

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Abstract

As climate and land-use changes threatens biodiversity, the identification of refugia areas for species becomes a crucial strategy in conservation planning. Here, we integrate climate change anomaly with a land-use change model both projected for 2050 to identify refugia areas for 103 bird species that occur in the Brazilian Cerrado. We found that 13% of the Cerrado may serve as refugia for the bird species. In contrast, nearly 35% of the biome might become areas of high risk for those species. Most species (74%) will held from 34% to 85% of their current geographic distribution in areas with less native vegetation, but with low climate anomaly. Apart from the protection of the refugia areas, we suggest restoration of native vegetation in regions that are likely to maintain climate conditions more adequate in the future. These areas should be prioritized to protect places with higher species richness and ease the establishment of corridors that would support climate-induced dispersal from high risk areas to suitable ones. Approaches that allow for the identification and future protection of refugia are fundamental to guarantee the conservation of biodiversity faced with climate change and rapid land-use changes that already taking place.

Keywords: Climate Anomaly; Environmental Suitability; Deforestation; Conservation Planning; Macrorefugia; Vulnerability.

Introduction

Climate change is a global threat to biodiversity, being pointed out as the main cause of species extinctions in the next decades (Dawson et al., 2011; Parmesan and Yohe, 2003; Thomas et al., 2004). It is expected that your effects will intensify once climate projections suggest an increase on global temperature of *ca.* 4.8 °C, depending on the scenario of greenhouse gases emissions till the end of this century (IPCC, 2013). Climatic changes cause variation in the phenology, geographic distribution and composition of ecological communities (Chen et al., 2011; Parmesan, 2006). Land-use change, via conversion, degradation, and fragmentation of habitats was and still is the main driver of biodiversity loss worldwide (Foley et al., 2005; Jetz et al., 2007; Newbold et al., 2015). It is expected that the combination of climate and land-use change increase even more the extinction rate projected to a near future (Brook et al., 2008; Jetz et al., 2007). For example, habitat loss and fragmentation can reduce the ability of species to change their distribution in pursuit of adequate climatic niches (Brook et al., 2008; Mantyka-Pringle et al., 2012).

Faced with the threats of climate and land-use change, an important strategy to the protection of biodiversity is to identify climatically adequate areas that will maintain suitable habitats for species in the future. One approach to identify these places consists on the use of climate change metrics for the identification of regions that are more or less exposed to these changes throughout time (Beaumont et al., 2011; Garcia et al., 2014; Loarie et al., 2009; Williams et al., 2007). Some examples of climate change metrics commonly used are the climatic anomalies, climatic extremes, and climate change velocity. Climatic anomalies and climatic extremes quantify the magnitude of change in the mean and extreme conditions, respectively, in a determined locality throughout time (Garcia et al., 2014). Climate change velocity is a measure of climatic dislocation rate in the landscape and provides a velocity with which species should move to pursuit their suitable climates (Loarie et al., 2009).

The scenarios of impact of environmental changes on biodiversity in the future focus in climate change and broadly neglects land-use changes (Titeux et al., 2016). Lack of projections that integrate the climate and land-use changes constitutes a great knowledge gap that prevents the development of more trusty scenarios for the implementation of biodiversity conservation policies in the future (Titeux et al., 2017, 2016). Thus, integrating land-use models with climate change metrics allow for the

identification of areas that can potentially act as climate and habitat refugia for biodiversity as well as establish more adequate conservation strategies for each area (Alagador and Cerdeira, 2018; Struebig et al., 2015; Triviño et al., 2018; Watson et al., 2013).

The identification and protection of potential refugia in landscapes is an important strategy for conservation planning in the context of global changes (Groves et al., 2012; Morelli et al., 2016; Ribeiro et al., 2018; Stralberg et al., 2018; Struebig et al., 2015). The occurrence of species is strongly affected by climate and their survival depends of the availability of their tolerated habitats, thus, species can face great risk if the climate conditions to which they are adapted to and their tolerated habitats disappear in the future (Garcia et al., 2014; Mantyka-Pringle et al., 2012; Newbold et al., 2015). Tropical species are particularly vulnerable to these changes, as they already live near their maximum thermal tolerance (Araújo et al., 2013; Khaliq et al., 2014), besides having high sensibility and low adaptation capacity (Foden et al., 2013). Owing to high rates of climate and land-use changes expected for the tropics (IPCC, 2013), it is probable that the extent of refugia areas will be the main mechanism by which the species could persist in the future (Reside et al., 2014), as these areas would hold climatic conditions as well as habitats that are more suitable for them.

Here we present a spatially explicit approach which incorporates both climate and land-use change models to identify areas of refugia for bird species in the Brazilian Cerrado. Specifically, our objectives were: (1) to identify major risk areas and possible refugia for bird species in the Cerrado; (2) to quantify the proportion of current geographic distribution of species within each of these areas, and (3) to point out likely conservation strategies according to the level of climate change and land-use in the region.

Methods

Study area and evaluated species

The domain of the Cerrado extends for 23% (200 million acres) of the terrestrial area of Brazil, being the second major biogeographic province of South America and the world's biggest savannah (Silva and Bates, 2002). It shows a considerable variation in its phytophysiology, which includes habitats ranging from open areas to forests of closed canopy (Eiten, 1972). The Cerrado is a Biodiversity Hotspot (Myers et al., 2000), being considered the world's most threatened savannah (Strassburg et al., 2017). Protected areas

cover 8.6% (Vieira et al. 2019) of the Cerrado and only 3% is legally protected by areas of integrated protection (Françoso et al., 2015). Other than the conversion of the major part of native vegetation due to strong farming pressure, the Cerrado finds itself in a predicted future high climate instability region, which makes the biodiversity particularly vulnerable to these changes (Borges et al., 2019; Watson et al., 2013).

The Cerrado shelters 856 bird species (Silva, 1995) of which 30 are endemic (Silva and Bates, 2002) and 56 are threatened according to Brazil's Red Book on Threatened Species (ICMBio, 2018). Bird species found in the Cerrado show very distinct patterns of geographic distribution, including those of endemic and strict distribution to wide-ranged species (cosmopolitan). Of the 856 species listed for the Cerrado, we included in this study only those species that have the largest proportion of their range within the biome. Species widely distributed in other biomes and having a small proportion of their distribution area within the Cerrado were excluded. Following this criterion, we select a subset of 103 bird species.

Climate and land-use data

To quantify the magnitude of local climate change we use standardized local anomalies. We calculated the sum of Standardized Euclidean Distances (SED) for temperature and precipitation between the current period (1960-1990) and 2050 (2041-2060) for each grid cell, according to Williams et al. (2007). Given that standardized local anomalies for temperature and precipitation may show a different spatial pattern, we adopted the same approach as Garcia et al. (2014), who have calculated these values individually. Further, a comparison both sets of results provides a better understanding of which parameter drives the patterns of combined temperature and precipitation change (see Garcia et al., 128 2014). To evaluate temperature, we use mean annual temperature (Bio1) and for precipitation we use annual precipitation (Bio12). SED differences between the current period and 2050 were standardized by the inter-annual standard deviation (current period) of temperature (seasonality of temperature - Bio4) and precipitation (seasonality of precipitation - Bio15) (Williams et al., 2007). We also calculated the SED for temperature and precipitation individually and standardized all SED values to range from 0 to 1. Higher values of SED indicate higher local climate change (Williams et al., 2007). The four bioclimatic variables mentioned above were obtained in the WorldClim database (Version 1.4; www.worldclim.org/version1) for the

present period and 2050 in the resolution of approximately 1 x 1 km (30 seconds latitude/longitude).

For 2050, we used climate projections of four General Atmosphere-Ocean Circulation Models – AOGCMs: CCSM4, MPI-ESM-LR, HadGEM2-AO and IPSL-CM5A-LR. These AOGCMs were chosen because they belong to groups of models with different predictions and covering the widest range of climatic predictions (Varela et al., 2015). We have chosen to use a scenario of high greenhouse gases emissions (RCP 8.5) compiled by the Coupled Model Intercomparison Project (CMIP) as a standard experimental protocol for studying the output of coupled AOGCMS (available at <https://esgf-node.llnl.gov/projects/cmip5/>). This seems to be a likely scenario given the trends for greenhouse gas emissions since the year 2000 and, besides, only minor differences have been noticed across all RCPs until 2050 (Diffenbaugh and Field, 2013; IPCC, 2013). To represent the value of each bioclimatic variable in 2050, we use the average of the four AOGCMs.

To evaluate land-use change, we used a map produced by Soares-Filho et al. (2016) projected for 2050. We cropped the map to the extension of the Cerrado and we put it in the same resolution of the climate variables (~ 1km x 1km), since that its original resolution is 500m x 500m. This spatially explicit model simulates the changes in land-use and the carbon emissions associated under diverse scenarios on the demand of agricultural land and deforestation policies for Brazil (for more details see Soares-Filho et al., 2016). We classified grid cells with different uses of land into two categories: “with more native vegetation” and “with less native vegetation”. Cells occupied by savannas, savannas in PAs, forests and forests in PAs were classified as having more nature vegetation (land use refugia), whereas cells occupied with other land uses (urban and agricultural) were classified as transformed (less native) vegetation.

Land-use and climate change integrated risk

To integrate the climate anomaly map with the land-use change map, we divided the climatic anomaly values into two categories: values above the median (high climatic anomaly) and values below the median (low climatic anomaly, i.e. climate refugia). Then, we overlapped the two maps to identify the regions with different combinations of climate and land-use classes (Fig. 1). In this paper, we define refugia as those areas that might have a combination of low projected climatic anomaly and also projected retention of

native vegetation until 2050. This is a wider understanding of refugia compared to its original definition, but justifiable as a way to include land-use changes on it.

We calculated the proportion of geographic distribution of each species and those listed as threatened by the national list that occurs inside each of the four regions presented in Figure 1. For that, we used the species range maps made available by BirdLife International (available at <http://www.birdlife.org/datazone/info/spcdownload>). Then, we rasterized species range maps and put them on the same resolution as our map which combines climate and land-use changes. Then, we calculated the proportion of species distribution area that occur inside each of the regions. We also calculated how much of refugia areas occur inside protected areas currently established in the Cerrado. Hereafter we refer to refugia as areas considered as both climate and land use refugia.

Results

Cerrado regions that were possibly exposed to higher values of climate anomaly (temperature + precipitation) would be localized in the north and northwest, and in smaller proportion in the south and southwest (Fig. 2a). Looking at patterns of temperature and precipitation changes separately; we observed an overlap of both regions in the north and northwest (Fig. 2b and c). A small portion in the west region would also be exposed only to the major values of temperature anomaly (Fig. 2b), while some patches in the center and portions of the southwest and south regions would be exposed only to the highest values of precipitation anomaly (Fig. 2c). Our land-use model projected for 2050 shows that the north region would concentrate the largest part of native vegetation, while south and west regions would be the ones losing more native vegetation (Supplementary material, Figure S1).

When we combined data from climatic anomaly and land-use changes, we found that 35.4% (~71 million hectares) of the Cerrado would be exposed to high climatic anomalies and poor native vegetation until 2050 (i.e. high-risk areas). High-risk areas are found in the north, northwest, middle, west and small areas in the south and southwest regions (Fig. 3a).

Areas likely to retain their native vegetation with low climatic anomaly (i.e. potential refugia), cover only 13% of the Cerrado. These areas are in the east part, from north to the south of the Cerrado (Fig. 3a). Areas with less native vegetation and with low climatic anomaly (37.5%) will be in the south between southeast and southwest, while

areas holding much native vegetation and high climatic anomalies (14%) will be in the middle between the north and western regions (Fig. 3a).

Nearly 74% of bird species will occur inside areas with less native vegetation, but with low climatic anomaly until 2050 (from 34% to 85% of their ranges; see Supplementary material, Table S1). Twenty-one species (20.4%) will keep from 30% to 69% of their distribution in areas with less native vegetation and high climatic anomaly. We found that only four species (*Celeus ochraceus*, *Asthenes luizae*, *Augastes scutatus* and *Embernagra longicauda*) will have most of their distribution (49% to 64%) in areas with native vegetation and low climatic anomaly (i.e. potential refugia) (Table S1). Almost 100% of the species (n = 94) will have a largest part of their distribution areas inside regions with less native vegetation, while 22.3% of the species will have a large part of their distribution areas inside the regions with high climate anomaly (Table S1).

Areas of high species richness (Fig. 3b) will fall outside future refugia. On average, the evaluated species will have 27% of their distribution in Region 1, 46% in Region 2, 12% in Region 3 and 15% in Region 4 (Fig. 4a).

Among studied species, 15 are considered threatened by the national list of threatened species. These species follow the same pattern of the total set, in which, on average, will have 31% of their distribution areas in Region 1, 44% in Region 2, 16% in Region 3 and only 9% in Region 4 (Fig. 4b). Four species (*Cercomacra ferdinandi*, *Paroaria baeri*, *Pyrrhura pfrimeri* and *Synallaxis simoni*) will be totally out of the refugia areas, being that the four are endemic and two of them (*C. ferdinandi* and *P. pfrimeri*) threatened (Table S1). Only 11.4% of the refugia areas occur inside protected areas.

Discussion

We combined projection of climate anomaly with a model of land-use change and identified refugia areas that safeguard bird species from negative impacts of environmental change over the next decades. We also showed that most species would be vulnerable as only a small part of their distribution would lie within protected refugia areas. Here we discuss these results and likely conservation strategies for regions with different combinations of climate and land-use change.

Identification of future biodiversity refugia areas is a fundamental strategy used by managers and conservation practitioners faced with the threat of environmental alterations. However, most studies based on this approach focus only on climate change

scenarios, neglecting land use changes (Titeux et al., 2016). As a consequence, decision makers end up having access to less trustworthy scenarios, because when land-use change is included in the analyses, predicted suitable areas for species change and/or reduce significantly (Struebig et al., 2015; Triviño et al., 2018).

Our approach showed that only 13% of the Cerrado will preserve habitat and stable climate conditions, being able to act as refugia for the species until 2050. Moreover, most species have large portions their distributions in high risk areas. Bird populations in these areas can be impacted in many ways: land-use change can increase population decline (Cavalcanti, 1999; Lopes et al., 2010) and increase predation and nest parasitism (Borges and Marini, 2010), local climatic changes can induce change in species' distribution, physiology and behavior, as well as alter the periods for activities such as migration and reproduction, favor the emergence of new diseases and biotic interactions, with negative consequences for the demography and dynamics of population (Crick, 2004; Sekercioglu et al., 2012). Further, it is known that species that inhabit tropical regions are particularly more vulnerable to climate change, once that they have already experienced near maximum tolerance levels of their temperature conditions (Araújo et al., 2013; Khaliq et al., 2014), have low capacity of physiological adaptation and plasticity (Araújo et al., 2013; Hoffmann et al., 2013). Due to differences in their biological and ecological traits, some Cerrado bird species would be more vulnerable to climate and land use changes than others (Borges et al., 2019).

We found that four species (*C. ferdinandi*, *P. baeri*, *P. pfrimeri* and *S. simoni*) will be the most vulnerable, as they occur totally outside refugia. These species should be prioritized for conservation and have their population monitored, especially because they are endemic to the Cerrado. *C. ferdinandi*, and *P. pfrimeri* are also threatened with extinction and were classified as highly vulnerable due to their high exposure and low responsiveness to climate and land use changes (Borges et al., 2019). *C. ferdinandi* and *S. simoni* will occur mainly in regions with more native vegetation and high climatic anomaly (Region 3, in Fig. 4), while *P. baeri* and *P. pfrimeri* have larger distribution in the region with high risk, i.e. less native vegetation and high climatic anomaly (Region 1, on Fig. 4). Because they occur in different regions, protecting these species demand different conservation strategies (Watson et al., 2013). With exception of *P. pfrimeri* that occurs in a thin band of dry forest, near Serra Geral, the other three species have overlapped distribution in the Araguaia River's hydrographic basin (del Hoyo, et al.,

2018). The preservation of these areas is critical, especially because habitat loss is the main threat to the populations of these species in the Cerrado (del Hoyo et al., 2018).

Different conservation strategies should be developed in regions likely to present different combinations of climate and land-use change (see Watson et al., 2013). For example, in areas with less native vegetation and high climatic anomaly, there is need for monitoring populations to identify current threats and identify the most vulnerable species that would demand more assisted conservation interventions, like future translocations to refugia areas. In areas with low suitability that pose risks to species permanence, management of the surrounding landscape to establish corridors and stepping stones which facilitate the movement and dispersal of species in search of suitable conditions is a priority action (Hole et al., 2011). In areas with less native vegetation but low climatic anomaly, restoration of those areas and their neighboring ones is important as a strategy to increase connectivity and increase the size of populations by facilitating species dispersal. In areas where native vegetation is abundant but might face high climatic anomaly, it would be important to reduce the existing threats and guarantee the preservation of that native vegetation so that the species have opportunities to adapt to local climate or disperse to refugia areas with more adequate climate. Finally, in areas with more native vegetation and low climatic anomaly, the creation of new protected areas and avoidance of current threats such as deforestation, wildfires and species invasion would guarantee the permanence of bird species in a shorter and a longer time period (Watson et al., 2013). These areas of refugia may require conflicting management actions, as they need to maintain viable populations of resident species, while at the same time, providing conditions that facilitate the settlement of new colonizers from unsuitable areas (Hole et al., 2011). The possibility of establishment of new communities with new sets of species need to be previously assessed with caution as, depending on species, it is likely to have significant impacts on local equilibria (Jackson and Sax, 2010). In order to encourage the protection of potential refugia areas, it is important to financially support landowners in preserving remnants of native vegetation through payment for environmental services, tax relief or other compensatory measures that are of interest to them.

Species-rich areas in the Cerrado overlap areas projected to lose native vegetation, but with low climate anomaly in the future (especially in southern Cerrado). Therefore, restoration becomes a fundamental strategy for the protection of Cerrado bird species. Currently 26% of the biome found in private lands must be restored to comply with the

Brazilian law on the protection of native vegetation (Vieira et al., 2018). It is already possible to develop a sustainable future for the Cerrado through the increase in productivity of cattle raising in the region and restoration of degraded pasturelands (Strassburg et al., 2017). This would save all of the necessary land for agricultural expansion, increase the production of bovine meat in 49% and still open 6.38 million hectares for restoration (Strassburg et al., 2017). The restoration of these areas is primordial to avoid not only the loss of the Cerrado's biodiversity, but also the loss of ecosystem services (Vieira et al., 2018). For areas in region 2 of our scheme (areas with less native vegetation and low climatic anomaly), it would be important to provide financial and fiscal incentives to landowners – especially smallholders – to support their compliance to the native vegetation law in Brazil. This compliance would be achieved mainly through restoration, and once these regions would have adequate climate conditions, restoring these regions would ensure the occurrence of resident species and also migrants arriving from regions of less suitable or even unsuitable climates.

Given the low resolution of the climatic models at our scale of analysis, it is not possible to evaluate if our refugia areas have local characteristics (e.g. streams, lakes, cold air drains and topographic exposure to radiation and wind) which could create microrefugia in an even thinner scale that could favor the species survival (Ashcroft, 2010; Gavin et al., 2014). However, for the species that present occurrences in more sparse areas such as birds, it is expected that the bigger scale refugia (macrorefugia) provide a better and sparser protection throughout time (Ashcroft, 2010). A caveat of our study is the spatially coarse definition of refugia, so that some specific sites within the defined refugia region may present important changes that some species will not be able to tolerate. However, the conservation strategies outlined for each of the four regions identified in our study are broad and generic suggestions rather than detailed and mandatory actions for a specific location (for an analysis considering the particular requirements for each species see, (Alagador et al., 2016). Approaches that are able to identify areas that are most suitable for species, considering the future threats of climate and land use changes, as presented here (see also Struebig et al., 2015; Triviño et al., 2018), remain critical to biodiversity conservation planning.

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Figure captions

Figure 1: Conceptual diagram showing the intersection between the climate anomaly and land-use projected for the Cerrado until 2050. *Region 1:* places with less native vegetation and high climatic anomaly – high risk; *Region 2:* places with less native vegetation and low climatic anomaly; *Region 3:* places with more native vegetation and high climatic anomaly; *Region 4:* places with more native vegetation and low climatic anomaly – refugia.

Figure 2: Climatic anomaly projected for the Cerrado until 2050. (a) Climatic anomaly (temperature + precipitation). (b) Temperature anomaly. (c) Precipitation anomaly.

Figure 3: Refugia and high-risk areas according to the climate and land-use changes projected for the Cerrado until 2050 (a) and present richness of bird species (b). *Region 1*: places with less native vegetation and high climatic anomaly – high risk; *Region 2*: places with less native vegetation and low climatic anomaly; *Region 3*: places with more native vegetation and high climatic anomaly; *Region 4*: places with more native vegetation and low climatic anomaly – refugia.

Figure 4: Mean and standard deviation in the proportion of the distribution area of the 103 evaluated species (a) and all threatened species (b) in each of the regions with the different combinations of climate anomaly and land-use.

Figure 1

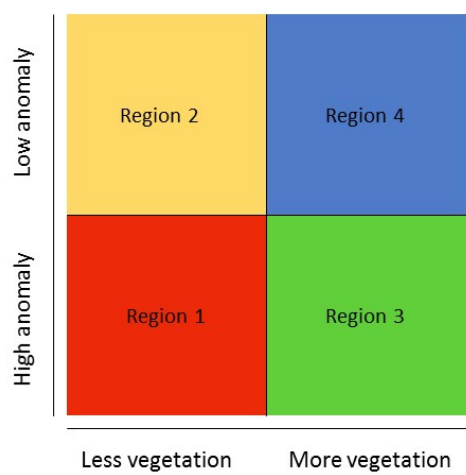


Figure 2

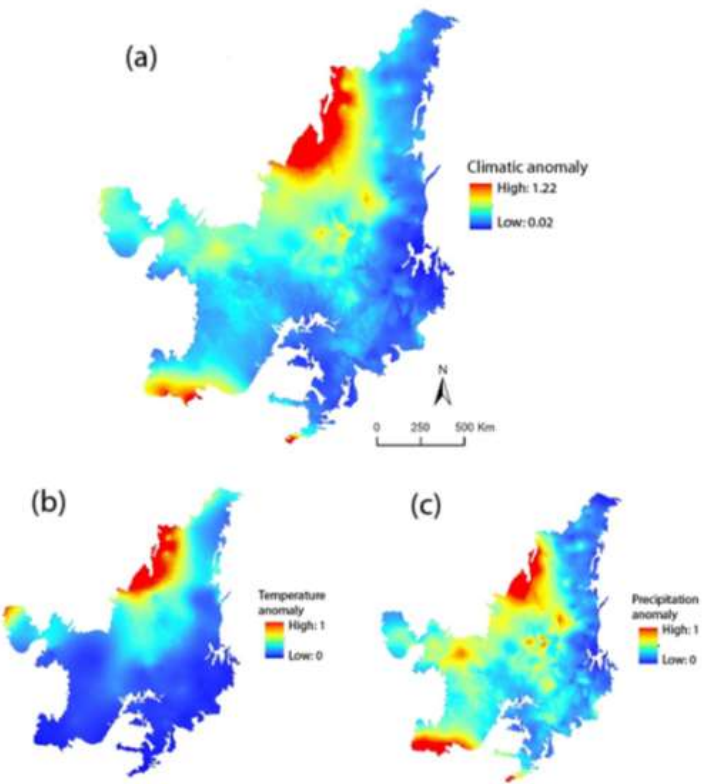


Figure 3

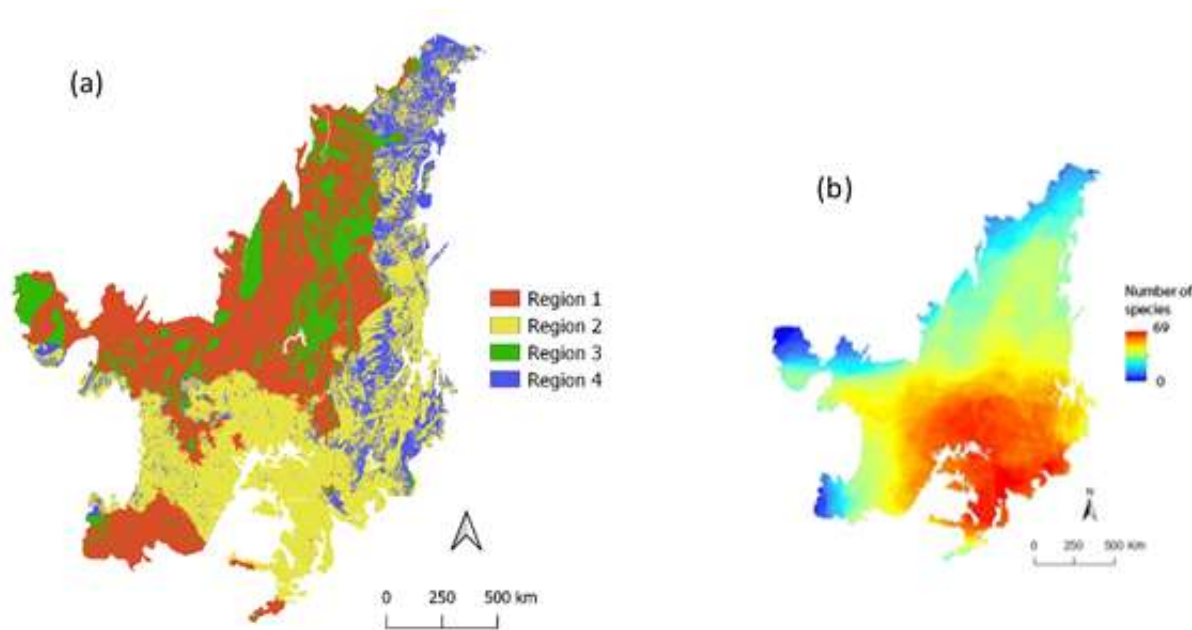
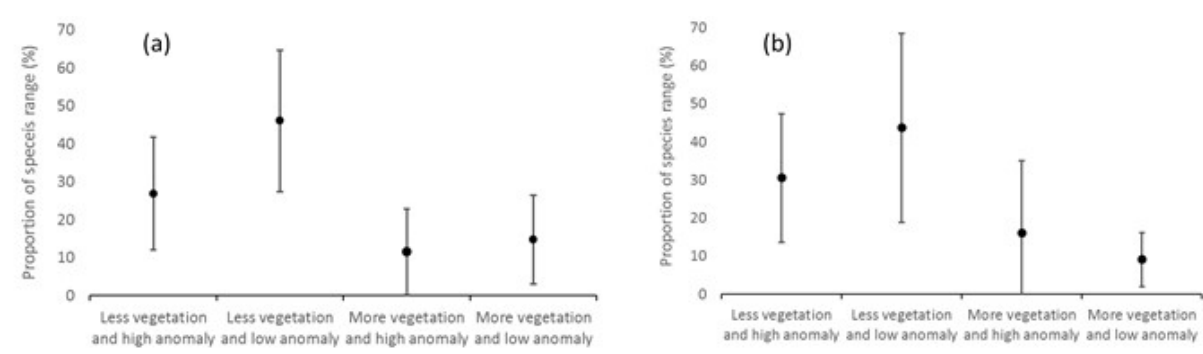


Figure 4

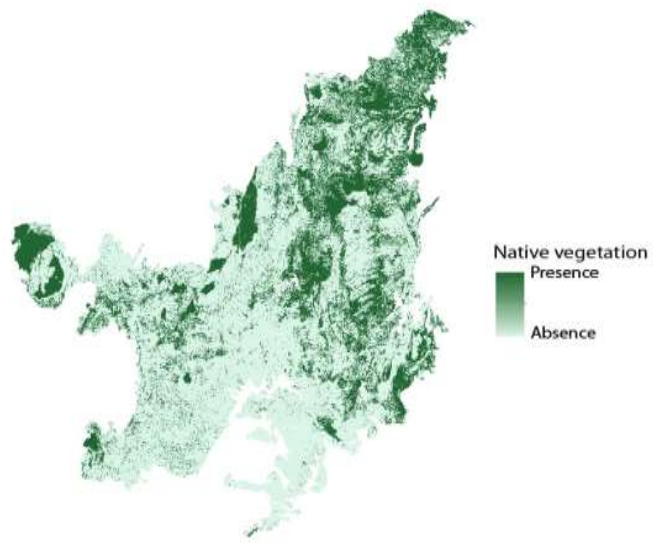


Supplementary material

Supplementary Table S1. Percentage of geographic range inside each of the regions identified in Figures 1 and 4a for all the 103 bird species studied.

Species	Region 1	Region 2	Region 3	Region 4
<i>Alipiopsitta xanthops</i>	38.93	35.84	14.47	10.32
<i>Amazilia lactea</i>	7.62	71.45	1.77	18.32
<i>Anodorhynchus hyacinthinus</i>	46.04	25.98	18.49	9.14
<i>Antilophia galeata</i>	37.85	38.88	13.80	9.06
<i>Aphantochroa cirrochloris</i>	13.19	68.71	3.31	13.97
<i>Aratinga auricapillus</i>	5.19	79.87	0.52	13.56
<i>Aratinga jandaya</i>	40.58	15.02	23.92	20.19
<i>Asemospiza fuliginosa</i>	34.08	40.27	18.77	5.20
<i>Asthenes luizae</i>	0.25	30.78	6.44	62.52
<i>Attila phoenicurus</i>	41.20	44.21	10.51	3.83
<i>Augastes scutatus</i>	0.19	37	4.68	58.12
<i>Automolus leucophthalmus</i>	17.53	72.57	1.77	7.41
<i>Baryphthengus ruficapillus</i>	8.91	72.92	1.34	16.07
<i>Casiornis fuscus</i>	34.82	23.34	19.97	21.31
<i>Celeus flavescens</i>	31.09	43.05	13.11	12.09
<i>Celeus obrieni</i>	46.87	16.91	24.87	10.79
<i>Celeus ochraceus</i>	0.05	35.01	0.31	64.27
<i>Cercomacra ferdinandi</i>	22.78	0	75.78	0.00
<i>Charitospiza eucosma</i>	34.61	39.03	13.11	12.71
<i>Clibanornis rectirostris</i>	21.33	60.58	5.24	12.37
<i>Columbina cyanopis</i>	31.20	58.06	5.55	5.13
<i>Compsothraupis loricata</i>	34.76	29.31	16.15	19.06
<i>Conopophaga lineata</i>	17.22	66.53	3.85	11.62
<i>Conothraupis mesoleuca</i>	45.38	29.16	16.09	9.35
<i>Cranioleuca semicinerea</i>	32.93	34.04	16.25	15.15
<i>Cyanocorax cristatellus</i>	36.73	38.99	13.49	10.30
<i>Cyanocorax cyanopogon</i>	32.48	35.59	14.89	16.46
<i>Cypseloides senex</i>	29.12	52.44	7.92	10.14
<i>Cypsnagra hirundinacea</i>	34.54	38.19	13.47	13.26
<i>Dendrocolaptes platyrostris</i>	27.38	45.7	11.45	14.89
<i>Diopsittaca cumanensis</i>	33.39	38.53	14.12	13.42
<i>Elaenia sordida</i>	16.94	66.48	3.45	12.56
<i>Embernagra longicauda</i>	0.10	48.2	2.49	49.17
<i>Eupetomena macroura</i>	31.86	41.17	12.15	14.30
<i>Eupsittula cactorum</i>	4.57	51.98	2.38	40.57
<i>Euscarthmus rufomarginatus</i>	34.71	40.96	13.11	10.77
<i>Fluvicola nengeta</i>	19.95	53.11	7.99	18.42
<i>Formicivora melanogaster</i>	27.89	50.69	6.12	14.95
<i>Furnarius figulus</i>	23.55	41.53	9.09	25.00
<i>Geositta poeciloptera</i>	22.87	56.51	8.48	11.52
<i>Heliactin bilophus</i>	32.80	39.9	13.69	13.12
<i>Heliomaster squamosus</i>	15.83	63.03	5.98	14.28
<i>Hemithraupis ruficapilla</i>	5.14	83.77	1.45	8.15
<i>Herpsilochmus atricapillus</i>	32.65	40.9	12.89	13.04
<i>Herpsilochmus longirostris</i>	44.34	34.4	16.24	4.64
<i>Hirundinea bellicosa</i>	34.90	37.85	13.85	12.88
<i>Hylophilus amaurocephalus</i>	9.00	63.05	2.74	24.36
<i>Icterus jamaicae</i>	29.88	28.42	18.36	22.88

<i>Ilicura militaris</i>	4.15	84.83	0.82	8.50
<i>Knipolegus franciscanus</i>	26.00	47.73	8.85	16.76
<i>Knipolegus lophotes</i>	29.82	47.89	13.11	8.34
<i>Knipolegus nigerrimus</i>	16.27	56.17	7.21	19.61
<i>Lepidocolaptes squamatus</i>	0.81	73.8	0.47	23.92
<i>Lophornis magnificus</i>	32.08	48.51	9.18	9.67
<i>Melanerpes flavifrons</i>	16.37	72.72	2.36	7.70
<i>Melanopareia torquata</i>	37.18	38.71	13.72	9.88
<i>Mergus octosetaceus</i>	18.25	66.3	6.67	7.90
<i>Microspingus cinereus</i>	32.66	48.12	8.42	10.32
<i>Myiothlypis leucophrys</i>	25.11	55.66	9.14	9.48
<i>Neopelma pallescens</i>	45.67	26.05	19.14	8.75
<i>Neothraupis fasciata</i>	28.29	46.99	10.23	13.93
<i>Nothura minor</i>	22.82	65.79	3.34	7.50
<i>Nyctiprogne vielliardi</i>	0.00	61.72	0.00	24.57
<i>Paroaria baeri</i>	64.15	3.17	32.59	0.00
<i>Paroaria dominicana</i>	1.01	52.99	1.08	44.20
<i>Penelope ochrogaster</i>	41.11	16.45	35.27	5.93
<i>Penelope supercilialis</i>	34.88	38.28	12.93	13.36
<i>Phaethornis nattereri</i>	48.99	14.51	20.56	15.58
<i>Phyllomyias fasciatus</i>	25.41	46.73	10.40	16.87
<i>Phyllomyias reiseri</i>	39.91	38.09	16.12	5.44
<i>Phylloscartes roquettei</i>	2.08	64.95	1.16	30.92
<i>Poecilotriccus fumifrons</i>	59.02	4.32	30.34	5.75
<i>Polystictus supercilialis</i>	0.39	68.32	1.23	29.16
<i>Porphyrospiza caerulescens</i>	29.06	41.12	12.71	16.63
<i>Primolius maracana</i>	37.67	38.66	13.84	9.31
<i>Pteroglossus inscriptus</i>	49.08	11.12	24.59	14.83
<i>Pyrrhura pfrimeri</i>	68.86	9.94	20.95	0.05
<i>Saltator atricollis</i>	30.55	42.73	11.84	14.36
<i>Schiffornis virescens</i>	17.33	70.77	1.85	9.40
<i>Schistochlamys ruficapillus</i>	29.55	42.05	12.90	14.87
<i>Sclerurus scansor</i>	25.48	56.46	6.70	10.72
<i>Scytalopus novacapitalis</i>	22.22	59.24	4.88	13.43
<i>Sirystes sibilator</i>	42.46	40.59	12.46	3.97
<i>Sporophila albogularis</i>	0.00	61.02	0.01	36.39
<i>Sporophila bouvreuil</i>	31.08	40.43	12.91	14.95
<i>Sporophila cinnamomea</i>	43.07	38.47	14.61	3.45
<i>Sporophila melanogaster</i>	15.33	74.51	2.98	6.38
<i>Sporophila palustris</i>	36.22	45.34	10.11	7.85
<i>Streptoprocne biscutata</i>	5.55	70.8	1.94	20.37
<i>Suiriri affinis</i>	40.38	35.15	16.31	7.70
<i>Synallaxis scutata</i>	33.00	39.2	13.72	13.56
<i>Synallaxis simoni</i>	27.02	0	69.23	0.00
<i>Syndactyla dimidiata</i>	33.01	47.54	9.69	9.22
<i>Tachyphonus coronatus</i>	26.37	64.12	2.67	5.88
<i>Tangara flava</i>	34.76	38.37	13.00	13.34
<i>Taoniscus nanus</i>	15.96	67.23	6.02	10.17
<i>Thalurania glaucopis</i>	34.41	56.86	3.17	4.61
<i>Thamnophilus pelzelni</i>	29.58	43.46	11.86	14.71
<i>Thamnophilus torquatus</i>	35.75	38.29	13.86	11.58
<i>Turdus subalaris</i>	35.85	49.54	7.10	7.02
<i>Uropelia campestris</i>	38.26	32.7	16.75	11.90
<i>Xiphocolaptes albicollis</i>	19.03	66.71	2.93	10.70
<i>Xiphorhynchus fuscus</i>	5.85	72.9	0.92	19.28



Supplementary Figure S1: Remnants of native vegetation in the Cerrado projected for 2050.

Critical areas for retaining the multiple dimensions of bird diversity in the Cerrado

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ABSTRACT

Taxonomic, phylogenetic and functional components of diversity in communities show different spatial patterns that respond to climate and land-use change and are geographically convergent, i.e. areas with high species richness usually hold also very different evolutionary lineages, for example. The opposite – known as biotic homogenization – can also occur, which means that some sites end up concentrating closely related lineages or species that perform very similar roles in the system. Here, we assessed current relationships among the taxonomic, phylogenetic, and functional diversity components and analyzes how expected changes in climate and land use may alter such patterns in bird communities inhabiting the Cerrado. In general, we found a high spatial inconsistency among the three diversity components. We found that the higher the number of species in a site the higher the number of different lineages it shelters. However, sites containing many species do not necessarily have more functional traits or species with playing different roles in ecosystems. We obtained higher values of beta diversity (i.e. turnover) for all diversity components in the transition zone between the Cerrado and the Amazon, while the remaining of the Cerrado had a low beta diversity. We also found that, owing to the changes in climate and land use, only a small set of areas is expected to lose several bird species, while most of the Cerrado will lose few. Because of such expected species loss, bird communities might become more clustered in the future – both phylogenetically and functionally – and only a few areas will be able to simultaneously safeguard the phylogenetic and functional diversity components of this group.

Keywords: Biodiversity conservation, Phylogenetic diversity, Functional diversity, Species distribution, Biotic homogenization.

Introduction

Studies on the diversity patterns of the ecological communities usually concentrate on the Taxonomic Diversity (hereafter, TD), normally measured through species richness (Pavoine and Bonsall, 2011). However, species richness *per se* does not provide much information for ignoring the fact that the species have different evolutionary histories and ecological functions. The Phylogenetic Diversity (hereafter, PD) reflects the evolutionary history of a community (Webb et al., 2002) and has an important influence on the productivity and stability of the ecosystem (Cadotte et al., 2012). Functional Diversity (hereafter, FD), in contrast, reflects the diversity of morphological, physiological and ecological traits inside the communities (Petchey and Gaston, 2006), representing the measure that best explains the functioning of the ecosystems (Hooper et al., 2005). Even though PD and FD can be positively correlated to TD (presence of more species can imply more traits and lineages of species; Losos, 2008), two communities with equal TD may strongly differ regarding their PD and FD (Arnan et al., 2015; Jarzyna and Jetz, 2017; Petchey and Gaston, 2006; Safi et al., 2011).

Environmental filters from certain habitats can select species with similar functional traits, resulting in communities that are functionally clustered (Díaz et al., 1998; Webb et al., 2002). In contrast, the competition for resources may favor the coexistence of species with different functional traits, thus generating functionally overdispersed communities (Pavoine and Bonsall, 2011). Environmental changes can interfere in the patterns of overdispersion and clustering of communities since communities in natural environments tend to be overdispersed, while communities in anthropized environments tend to be more clustered (Frishkoff et al., 2014). In addition, several studies have pointed out that regions with high TD can be inconsistent with regions with high PD or FD and that such spatial incompatibility among the different diversity components may result in conservation strategies that do not represent biodiversity in its entirety (Cumming and Child, 2009; Devictor et al., 2010; Forest et al., 2007; Strecker et al., 2011; Thuiller et al., 2014b; Tucker et al., 2012).

Climate and land-use changes are currently the main causes of fast loss of global biodiversity and may lead to lower abundance, extinction of species, and alterations in the structure of communities (Bellard et al., 2012; Pereira et al., 2010). The way in which species respond to the changes in climate and land use can alter not only species composition, but consequently the phylogenetic and functional structures in the

communities and potentially affect the provision of ecosystem services (Arnan et al., 2018; Flynn et al., 2011; Hidasi-neto et al., 2019; Liang et al., 2019; Nowakowski et al., 2018; Thuiller et al., 2014b). These global changes can act as a filter capable to reduce the taxonomic, phylogenetic and functional diversity components in the communities leading to biotic homogenization (Clavel et al., 2011; Newbold et al., 2019). Based on this, it is extremely important that the conservation planning is carried out to integrate the different components of biodiversity, reflecting their taxonomic, phylogenetic, and functional aspects.

Birds play a series of ecological functions among vertebrates and represent important moving bonds in the dynamics of ecosystems contributing to their functioning and service provision (Sekercioglu, 2006; Whelan et al., 2008). The ecological roles performed by birds include the dispersion of seeds, pollination, predation of invertebrates and vertebrates (population control), carcass removal, recycling and deposition of nutrients, engineering of ecosystem, and contribution to cultural and economic services (Sekercioglu, 2006; Whelan et al., 2008). The changes in climate and land can affect bird communities and lead to the loss and replacement of species, consequently compromising the performance of some services ecosystem (Devictor et al., 2008; Frishkoff et al., 2016; Ibarra and Martin, 2015).

Considering that the bird species would cease to occur in sites where the climate conditions would exceed their current tolerance limits and simultaneously lose their native vegetation, we assessed how climate and land use changes projected until 2050 would affect the patterns of taxonomic, phylogenetic and functional diversity of the birds in Cerrado. Specifically, we had the following objectives: (1) to verify whether the phylogenetic and functional structures relate to the taxonomic diversity and between each other by assessing how these components distribute spatially, (2) to assess the effects of the climate and land use changes on species loss and the phylogenetic and functional structure in the bird communities, and (3) to map important areas for the conservation of the taxonomic, phylogenetic, and functional diversity components of birds in the Cerrado regarding the changes in climate and land use projected until 2050.

Methods

Study area and species assessed

The Cerrado domain covers 23% (~ 2 million km²) of the land surface in Brazil, which represent the second largest biogeographic province in South America and the largest tropical savanna in the world (Silva and Bates, 2002). It presents a considerable variation in its phytophysognomy ranging from open fields to closed canopy forests (Eiten, 1972). Cerrado is the most threatened savanna in the world and has protected areas covering 7.5% of the biome, out of which only 3% are under integral protection (Françoso et al., 2015; Strassburg et al., 2017; Vieira et al., 2018). In addition, Cerrado is located in a region of high climate instability and loss of native vegetation, which may present high concentrations of species that are vulnerable to global changes (Watson et al., 2013). Climate projections for the Cerrado indicate an increase in the temperature from 5 to 5.5° C and a decrease in the rainfall between 35% and 45% (PBMC, 2013). Additionally, around 31% to 34% of the remaining native vegetation in Cerrado can be lost until 2050, mainly due to weak protection and strong pressure for agricultural expansion (Soares-Filho et al., 2016).

There are 856 bird species registered for the Cerrado (Silva, 1995), out of which 30 are endemic (Silva and Bates, 2002) and 32 are endangered according to the Brazilian list of endangered species (ICMBio, 2018). The bird species found in the Cerrado present very distinct patterns of geographic distribution, ranging from endemic species, those of restricted distribution to cosmopolitan species. In our study, we considered only the species presenting most of their distribution in the Cerrado and discarded those occurring only marginally. Therefore, our final list includes 577 bird species. We obtained the data on the area of occurrence of the 577 species through the geographic distribution maps disposable on BirdLife International (available on: <http://www.birdlife.org/datazone/info/spcdownload>). These maps allowed us to generate matrices of presence/absence of the species by overlapping them in a grid of 0.5° x 0.5°. The species were considered present in the cell if its distribution overlapped any part of the cell.

Data on climate and land use

We retrieved bioclimate variables for the current period (1960-1990) and 2050 (2041-2060) from the database WorldClim (version 1.4; www.worldclim.org/version1) (Hijmans et al., 2005). For 2050, we used the climate projections of 15 Models of General Circulation of the Atmosphere and Ocean (AOGCMs: ACCESS1-0, BCC-CSM1-1, CCSM4, CNRM-CM5, GISS-E2-R, HadGEM2-AO, HadGEM2-CC, HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM-CHEM, MIROC-ESM, MIROC5, MPI-ESM-LR, MRI-CGCM3, and NorESM1-M) for a scenario of high concentration of greenhouse effect gases (RCP 8.5, IPCC, 2013). This seems to be the most likely scenario considering the tendency of emissions of greenhouse effect gases since 2000; in addition, only minor differences appear among all the RCPs until 2050 (Diffenbaugh and Field, 2013; IPCC, 2013). To prevent collinearity issues among the 19 bioclimate variables, we developed a factorial analysis to choose those that explain the highest variation of data. The following bioclimate variables were selected to quantify the exposition of bird species to climate change: 1) Diurnal variation in mean temperature (BIO2); 2) Temperature seasonality (BIO4); 3) Mean temperature in the hottest trimester (BIO10); 4) Rainfall in the wettest trimester (BIO16), and 5) Rainfall in the driest trimester (BIO17).

We assessed climate exposition by quantifying the species distribution area in which the climate conditions in 2050 would exceed the climate amplitude experienced by the species in the current period. Current climate conditions of each of the five bioclimate variables abovementioned were used to determine the amplitude (maximum – minimum) to which each species is currently exposed inside their current distribution. In each cell of the grid, we calculated the mean and the standard deviation of the projections derived from the 15 AOGCMs for the five bioclimate variables. To represent the value of each bioclimate variable in 2050, we used the mean of the 15 AOGCMs minus a standard deviation (see Ribeiro et al., 2016). Thus, the species were considered absent in the grid cells in which the climate conditions in 2050 would exceed the climate amplitude currently experienced by them.

To evaluate change in land use, we used the maps produced by Soares-Filho et al. (2016) for the period of 2012 and projected for 2050 at a resolution of 500 m. We then resampled the map to produce another one with the resolution of 0.5° x 0.5°, compatible with our climatic data. We considered a threshold above 50% (e.g. whenever more than 50% of the smaller cells had native vegetation, the larger cell was classified in the native

vegetation category). This spatially explicit model simulates the change in land use and carbon emissions associated with many scenarios of agricultural lands demands and deforestation policies for Brazil (for further details, see Soares-Filho et al. 2016). Therefore, we classified the cells in the grid according to the different land uses into two categories: “with native vegetation” and “without native vegetation”. The cells occupied with savannas, savannas in protected areas, forests and forests in protected areas fit the “with native vegetation” category, while the cells occupied with other types of soil use (urban and agricultural) fit the “without native vegetation” category. The species were regarded as present in the cells that would maintain the native vegetation until 2050 and absent in the cells occupied with native vegetation in 2012 but converted into other uses until 2050.

Biological traits and phylogeny

To quantify functional diversity, we considered the following biological traits: diet, regarded as the estimated percentage for each diet item (invertebrates, vertebrates, scavengers, fruit, nectar, seeds, and plants); foraging space, regarded as the estimated percentage of time spent per stratum (soil, sub-wood, medium-high, crown, and air), foraging period, regarded as binary category variable (diurnal and nocturnal), and body mass (in grams), regarded as continuous variable. These traits were obtained for all species in Wilman et al. (2014). The traits used in this study are related to the acquisition of resources and define important dimensions of the species niche, in addition to having important bonds to the functioning of the ecosystems (Sekercioglu, 2006).

To quantify the phylogenetic diversity, we first used the phylogenetic hypothesis produced by Jetz et al. (2012). As the authors did not provide a consensus phylogeny, we produced a Maximum Clade Credibility (MCC) tree from 9999 random phylogenies, complete and dated, using software TreeAnnotator v1.8.1 of package BEAST (Drummond et al., 2012). The resulting consensus phylogeny was applied for all subsequent phylogenetic analyses.

Taxonomic, functional, and phylogenetic alpha and beta diversities

The alpha taxonomic diversity was estimated as the number of species present in each grid cell in the two scenarios assessed. To calculate functional diversity (FD;

Petchey and Gaston, 2006), we built a functional distance matrix containing the species in the lines and the traits in the columns. Since our matrices of traits included different types of traits, we used a modification of the Gower distance (Pavoine et al., 2009) to produce matrices of distance and the unweighted pair group method with arithmetic means to produce the functional dendrograms for the 577 bird species assessed. FD is a measure of functional diversity based on the dendrogram that quantifies the extension of the complementarity among the values of the traits of the species by estimating the dispersion of the species in the space of the traits. Greater differences among the values of the traits of the species represent higher complementarity of the traits and higher FD. We used the phylogenetic diversity index (PD; Faith, 1992) to quantify the phylogenetic diversity of the communities. PD is a continuous measure that assesses the relationship of the species by using the sum of the length of the branches of the phylogenetic tree that connects all species in a community.

As PD and FD can depend on the species richness, we measured the Size of the Standardized Effect (SES) for PD and FD by comparing the values found for each one with the values generated randomly (999 randomizations) altering the “label taxa” at the edges of the functional dendrogram and the phylogenetic tree and maintaining the species richness observed for each focal community. We calculated the SES in the following manner: $SES = (obs - rnd) / sd.rnd$, in which obs is the value found for PD or FD, rnd is the mean value of the 999 randomizations and sd.rnd is the standard deviation of the 999 random values. Therefore, positive values of the SES indicate that the phylogenetic or functional diversity is higher than expected randomly (superdispersion), while negative values indicate lower than expected randomly (clustering). We used the SES PD and SES FD to represent, respectively, the phylogenetic structure (diversity of lineages) and functional structure (diversity of functional traces) of the bird communities in the Cerrado.

For the beta diversity, we calculated the Jaccard dissimilarity (β_{JAC}) of multiple sites (Baselga, 2013) and partitioned it in their turnover (β_{JTU}) and nesting (β_{JNE}) components using the package betapart (Baselga, 2010; Baselga and Orme, 2012). This study considers only the turnover component of beta diversity in the analyses, therefore, we calculated the beta taxonomic diversity as the turnover component of the Jaccard index between a focal cell and its eight adjacent cells (Baselga, 2013; Baselga and Orme, 2012). We calculated the beta phylogenetic diversity using the same process as in the taxonomic component, but applying the phylo.beta.multi function that computes the partition of

turnover through UniFrac index (Baselga and Orme, 2012). This same process was also applied to calculate the beta functional diversity, but using Gower distance and unweighted pair group method with arithmetic mean (UPGMA) to generate a functional dendrogram, which was applied to calculate the mean turnover between a focal cell and its neighbors.

To verify whether climate and land use changes will affect the taxonomic component and the phylogenetic and functional structures in the bird communities in the Cerrado, we compared the values of TD, SES PD, and SES FD found for the current period with those projected for 2050. We used the matrices of presence/absence of the species built for both scenarios (present and future) to calculate the taxonomic diversity and phylogenetic and functional structures in the bird communities in the Cerrado. Since our approach considers that the species would not occur in cells that would lose their native vegetation and simultaneously have climate conditions outside the currently tolerated value, it is not possible that the gain in species between the two scenarios occurred. The cells in the grid can only maintain or lose their currently existing species.

Considering that both PD and FD are correlated to species richness and that areas with few species of different lineages or with different functional traits can have high values of SES PD or SES FD, we sought to map areas that would have an overlap of the highest values of these two measures (areas with high phylogenetic or functional diversity and higher values than expected randomly). Overlapping areas with the highest values of PD and SES PD were considered of high importance for the conservation of the phylogenetic component, while the overlap areas of the highest values of FD and SES FD were considered of high importance for the conservation of the functional component. We also sought for areas that could present a coherence among the sites with higher phylogenetic diversity than expected randomly (SES PD) and higher functional diversity than expected randomly (SES FD) considering the climate and land use changes until 2050.

Spatial analyses

To verify the relationships among the diversity components, we applied non-generalized linear models that consider the spatial dependence among the samples. We used a structure of simultaneous autoregressive covariance (SAR) with a matrix of weights in which the sum of all weights equals 1. We built the weight matrix from a

matrix of immediate neighbors of the cells and adjusted the lambda parameter to set the weight matrix to the spatial structure of the residues by using the function *spautolm* in package *spdep* (Bivand and Wong, 2018). All calculations were generated on software R (R Development Core Team, 2018).

Results

We found a positive relationship between species richness and the phylogenetic structure of the bird communities, indicating that the poorest communities were clustered phylogenetically, while the richest ones tend to be overdispersed ($R^2 = 0.02$, $p < 0.001$; Fig. 1a). In contrast, the relationship between species richness and the functional structure of the bird communities proved negative, indicating that the poorest communities were overdispersed, while the richest ones were clustered functionally ($R^2 = 0.28$, $p < 0.001$; Fig. 1b). The relationship between the phylogenetic structure and the functional structure of communities proved negative ($R^2 = 0.01$, $p < 0.001$) with a very low association between them. The taxonomic diversity and the phylogenetic and functional structures showed different spatial patterns (Fig. 2a, d, and g). In general, the taxonomic diversity concentrates in the south and southwest regions, with the lowest values occurring in the north, the diversity of lineages was higher in the extreme south and east, while the diversity of functional traits proved higher in the north and northwest regions of Cerrado (Fig. 2a, d, and g) – an almost opposite pattern to the taxonomic diversity. In other words, the congruence among the three components of bird alpha diversity was rather low.

The beta diversity had a congruent spatial pattern among the three diversity components (Fig. 2c, f, and i) with the highest turnover values concentrated in the north region, which has the lowest species richness (Fig. 2a), while the remaining of Cerrado presented rather low turnover values. In general, the taxonomic turnover was higher and had a more marked spatial pattern than the phylogenetic and functional turnover, while the functional turnover variation was relatively the lowest one, indicating that the functional traits used in this study are distributed throughout the Cerrado.

Considering a scenario in which bird species would not be able to adapt in sites whose climate conditions would exceed the maximum limits currently tolerated and simultaneously lose native vegetation to other human impacts, 16 cells from our study area would lose all species until 2050 (Fig. 2b). Approximately 6% of the Cerrado (51 grid cells) would lose over 90% of the bird species currently present. The mean reduction

in bird species richness until 2050 was -38 ± 90 species per grid cell. Spatially, species loss concentrates on a few cells in the center-north region of Cerrado. In general, few cells would lose many species, while most cells would lose relatively few species until 2050 (Fig. 2b).

Changes in climate and land use would cause the clustering to increase (negative values) and the overdispersion to reduce (positive values) between the values of SES for the current and the future periods, either for the phylogenetic structure (SES PD present: -1.65 to 1.84, SES PD future: -3.28 to 1.18; Fig. 2d and e) and the functional structure (SES FD present: -1.85 to 2.37, SES FD future: -2.95 to 2.10; Fig. 2g and h). This means that in 2050 more cells in the study area would have a lower diversity of lineages and functional traits than expected, as well as less cells would have a greater diversity of lineages and functional traits than expected randomly (the communities would become more closely related and functionally similar to each other).

Important areas for the conservation of the phylogenetic component (higher values of PD and SES PD, red color; Fig. 3a) would be located at the south edge of the Cerrado encompassing the borders of the southeast, south, and southwest regions. In contrast, the areas with the lowest values of PD and SES PD (green color; Fig. 3a) would concentrate on the north region with some areas in the center and west of Cerrado. Important areas for the conservation of the functional component (higher values of FD and SES FD, red color; Fig. 2b) would concentrate on a range from the center to the west of Cerrado. In turn, areas of low importance for the functional component (green color; Fig. 3b) would spread in the south region to the east, in the center and north of Cerrado. In general, the important areas for the conservation of the phylogenetic and functional components do not coincide with the areas of larger proportions of species loss (Fig. 3a e b). The colors yellow and blue represent intermediate areas regarding the importance for the conservation of the phylogenetic (Fig. 3a) and functional (Fig. 3b) components of the birds in the Cerrado.

According to our results, congruent areas with a high diversity of lineages and functional traits would concentrate more in a small portion of the west and with some cells spread in the center, east, and borders of the south (red color; Fig. 3c). In contrast, congruent areas with lower values of diversity of lineages and functional traits would concentrate in the center-south of the Cerrado (green color; Fig. 3c).

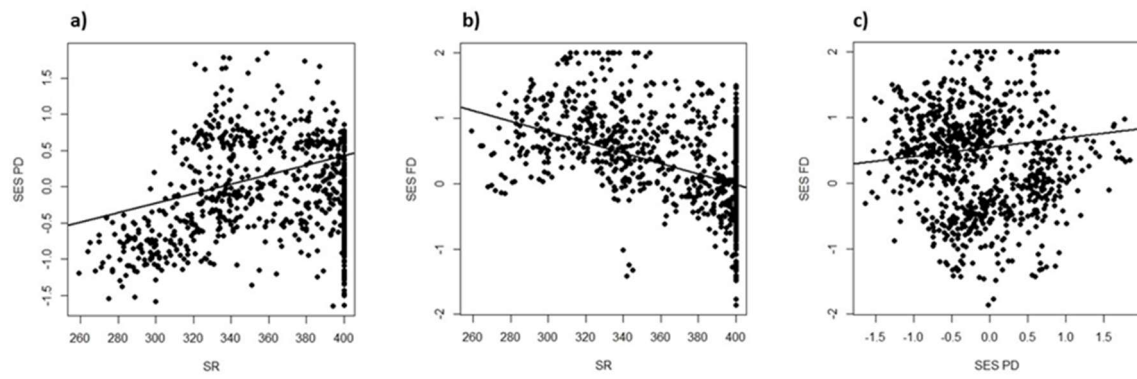


Figure 1. Relationship between the components of alpha diversity. SR: Species Richness; SES PD: Phylogenetic Standardize Effect Size; SES FD: Functional Standardize Effect Size.

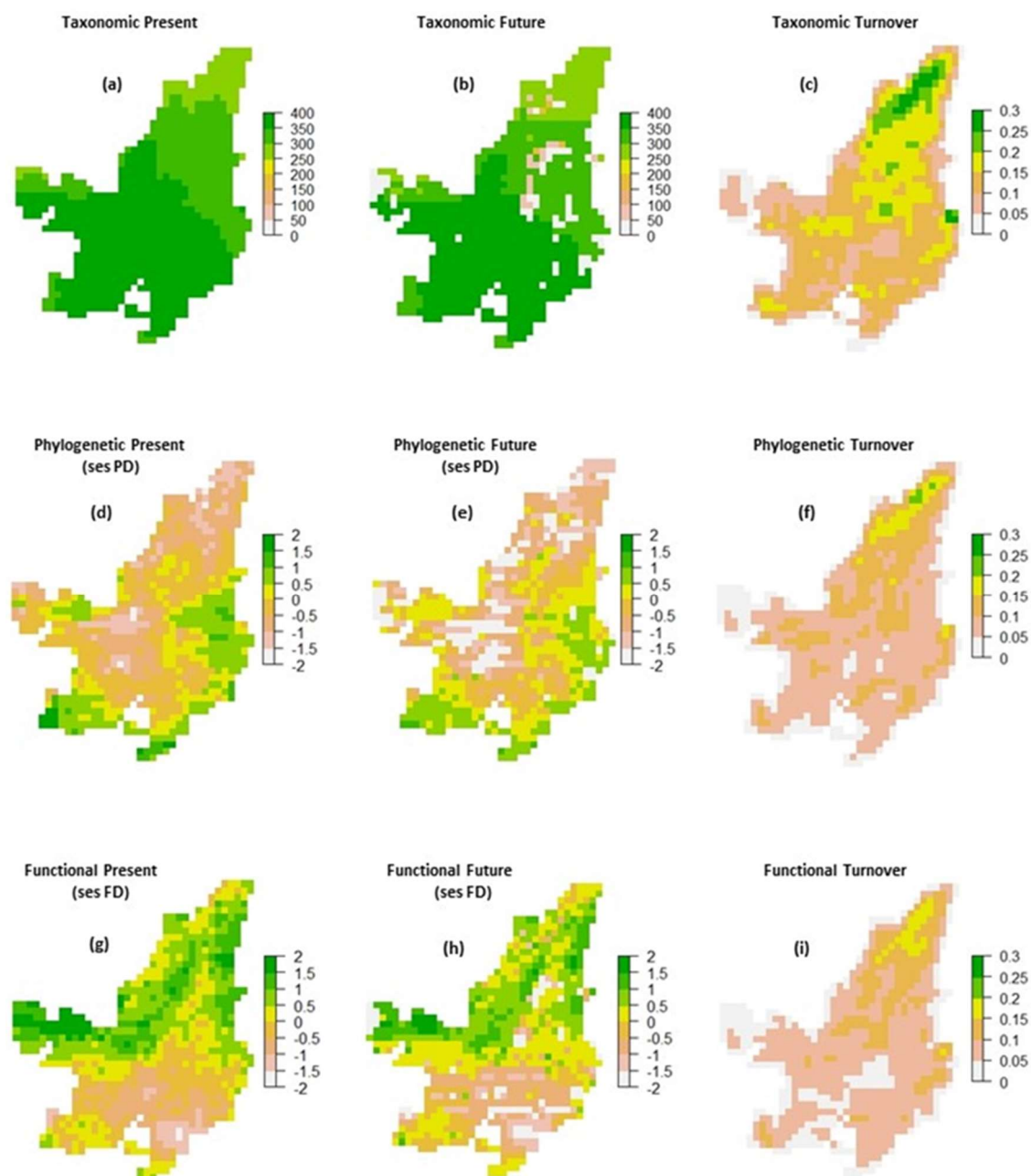


Figure 2. Maps indicating the spatial pattern for species richness in the present (a) and in the future (b), taxonomic diversity turnover (c), values of phylogenetic structure for the present (d) and for the future (e), phylogenetic diversity turnover (f), values of functional structure for the present (g) and the future (h), and functional diversity turnover (i).

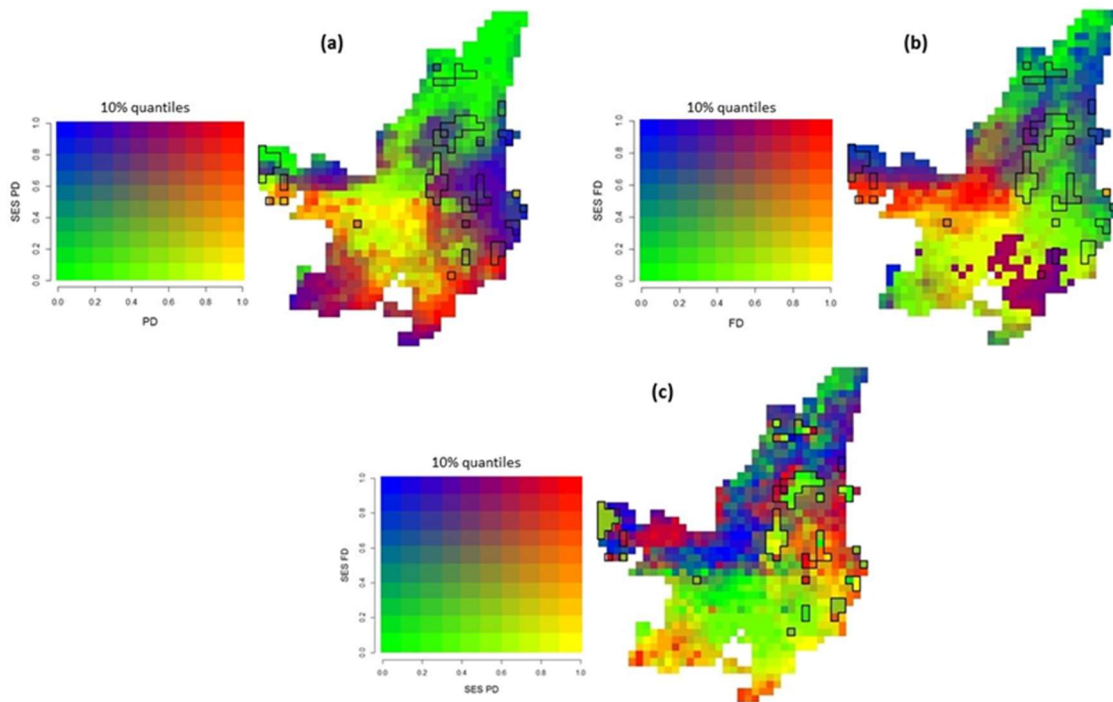


Figure 3. Maps illustrating the relationship between the phylogenetic diversity (PD) and the size of the phylogenetic diversity effect (SES PD) (a), relationship between functional diversity (FD) and the size of the functional diversity effect (SES FD) (b) relationship between the size of the phylogenetic diversity effect (SES PD) and the size of the functional diversity effect (SES FD) (c) in the future. Cells surrounded by the black line correspond to the areas with the highest proportions of species loss. In b, c and d, each color change means a 10% quantile shift in our variables. Red areas indicate the most important regions for the conservation of phylogenetic (a), functional (b), and both (c) diversity in the Cerrado.

Discussion

This study demonstrates that, in the Cerrado, the phylogenetic structure was positively related to taxonomic diversity, while the functional structure presented a negative relationship. The phylogenetic and functional structures had a negative relationship, but weakly correlated. For beta diversity, excluding a few areas in the north of Cerrado, the remaining of the biome already presents a certain degree of homogenization of TD, PD, and FD. We found that the climate and land use changes could cause a species loss disproportionately concentrated in a few areas in the center-north of Cerrado, coinciding with some sites of higher turnover. In general, we showed that a low overlap would occur between the regions with the highest values of diversity

taxonomic, lineages, and functional traits. Our results point out that the species loss caused by the changes in climate and land use would make the bird communities more phylogenetically and functionally clustered until 2050. Finally, we indicate that the important areas for the conservation of the phylogenetic and functional components in the future would occur in small regions of the Cerrado with low spatial overlap among them.

Our results show a high spatial inconsistency between species richness and the phylogenetic and functional components of diversity in the communities. In fact, some studies reveal that regions of high taxonomic diversity can be inconsistent with regions of high phylogenetic or functional diversity (Cumming and Child, 2009; Devictor et al., 2010; Forest et al., 2007; Strecker et al., 2011; Thuiller et al., 2014a; Tucker et al., 2012). Such low congruence among the three diversity components suggests the occurrence of a variation in the types of functions and evolutionary history that result in unique species combinations that cannot be entirely explained by examining species richness (Brum et al., 2017; Strecker et al., 2011); in addition, environmental factors may independently affect each diversity component (Webb et al., 2002). Thus, similarly to some previous studies, our results suggest that considering species richness exclusively can result in conservation strategies incapable of representing biodiversity in its different dimensions; in addition, a component is not a proper substitute to represent the remaining ones (Brum et al., 2017; Devictor et al., 2010; Strecker et al., 2011). For example, our results indicate that the northern areas of Cerrado contain species with higher levels of functional distinction, but they are not regarded as high conservation priority when considering the diversity of lineages.

Regarding beta diversity, we found a considerable spatial congruence among the three diversity components. Thus, also corroborating the findings of other studies regarding beta diversity, changes in the phylogenetic and functional compositions of the communities demonstrated to be related to the change in species composition (Arnan et al., 2015; Corbelli et al., 2015; Devictor et al., 2010; Liang et al., 2019; Pool et al., 2014). Except for the extreme north, the remaining of the Cerrado presented very low values of beta diversity for the three components. In fact, in the New World the beta diversity is low for birds in plain areas, such as the Cerrado (Melo et al., 2009).

Our results suggest that the climate and land use changes could act as a filter capable of altering the phylogenetic and functional structures of the communities by removing species from different lineages and with distinct ecological functions. In fact,

some studies demonstrate that the changes in climate and land use may reduce the phylogenetic and functional diversity of the communities leading to the homogenization of these components (Arnan et al., 2018; Devictor et al., 2008; Flynn et al., 2009; Frishkoff et al., 2014; Hidasi-neto et al., 2019; Jarzyna and Jetz, 2017; Liang et al., 2019; Nowakowski et al., 2018; Thuiller et al., 2014a, 2011). Consequently, the homogenization can lower the long-term evolutionary potential of the communities of species or reduce the services provided by the influenced ecosystems (Clavel et al., 2011; Olden et al., 2004).

Considering the spatial inconsistency among the three diversity components found here, an integrative approach proves essential to overcome the challenge of establishing conservation strategies to prioritize not only species richness, but also the functioning of ecosystems and the evolutionary history of the biota (Devictor et al., 2010; Hidasi-neto et al., 2019; Jarzyna and Jetz, 2017; Liang et al., 2019; Thuiller et al., 2014a). The areas we found to be important for bird conservation are in accordance with a study that assessed the impacts of changes climate on the communities of mammals in the Cerrado and found that areas with high species richness and phylogenetic diversity would occur in the south, while those with higher functional diversity would extend from the center to the west and to the north (Hidasi-neto et al., 2019).

Our results also indicated that the south and southeast of the Cerrado would shelter important areas for the conservation of the phylogenetic component, some areas that would be simultaneously important for the phylogenetic and functional component, in addition to maintaining a high species richness in the future. However, the south of the Cerrado as a whole is its best developed and most populous region, where around 85% of the native vegetation has already been converted, especially in pastures and plantations, and the remaining is highly fragmented (Sano et al., 2010; Strassburg et al., 2017). Therefore, landscape restoration in these areas becomes a fundamental strategy for the conservation of the different diversity components of birds in the Cerrado. In fact, some studies demonstrate that restoration would be a priority strategy for the conservation in Cerrado, which would be able to prevent the extinction of endemic plants (Strassburg et al., 2017), create new habitats for endangered species and enhance ecosystem services (Vieira et al., 2018), guarantee habitats in regions with more adequate climate conditions for the birds (Borges and Loyola, under review), and prevent the phylogenetic and functional homogenization of the communities of mammals (Hidasi-neto et al., 2019).

In this study, we considered that the bird species would cease to occur only in sites that would lose their native vegetation and concomitantly have climate conditions outside the currently tolerated limit. We assumed that the species would be able to adapt and persevere in sites where they would be exposed only to climate change or only land use change. We understand that our results depend on such consideration, however, some evidence suggests to consider that a combined effect of these two threats represents a better approach than regarding them separately (Arnan et al., 2018; Frishkoff et al., 2016; Newbold et al., 2019; Oliver and Morecroft, 2014). Furthermore, the changes in climate and land use are expected to favor the same species, which could lead to the homogenization of biodiversity in a more severe manner than expected (Frishkoff et al., 2016; Newbold et al., 2019)

Conclusion

Our results reinforce the need of an integrative approach among the three biodiversity components to assure the protection of species in order to preserve the ecosystem functioning and the evolutionary history of the biota. There is a spatial incongruity in the current patterns of taxonomic diversity and the phylogenetic and functional structures; in addition, as long as the phylogenetic structure is positively related to species richness, the functional structure presents a negative relation.

We found that the species loss caused by climate and land use changes would make the bird communities in the Cerrado more phylogenetically and functionally clustered in the future. Furthermore, important sites for the conservation of the phylogenetic and the functional component would occupy small areas in the Cerrado with low congruence among them, which hampers the selection of conservation areas.

Even more worrying is the fact that the important conservation areas for the taxonomic, phylogenetic and functional components would occur in the most anthropized region, where the remaining habitats are highly fragmented. Therefore, conservation plans for the Cerrado should prioritize actions to guarantee the permanence of species in these areas, such as landscape restoration and connectivity.

Our study highlights the important aspects of the relationships among the three diversity components by providing important grounds for a spatial planning of conservation and considering the three diversity components as a set, in addition to

introducing a wider discussion on the impacts of climate and land use changes on biodiversity.

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Conclusões

As mudanças climática e de uso da terra são apontadas como os principais impactos humanos como ameaça a biodiversidade atualmente e no futuro. Nesse contexto, nesta tese discuti os mecanismos de respostas das espécies, identifiquei as espécies mais vulneráveis, apontando os fatores responsáveis pela sua vulnerabilidade, mapeei áreas importantes para a conservação das espécies e avaliei como essas duas ameaças podem afetar os componentes taxonômico, filogenético e funcional da diversidade. Apresentei e discuti estratégias de conservação importantes para ampliar o conhecimento científico e também apoiar a tomada de decisão em planos de conservação. Espero que as abordagens descritas ao longo dessa tese possam ajudar os tomadores de decisão a embasar políticas de conservação mais adequadas.

Os resultados apresentados nesta tese apontam para as principais conclusões a seguir:

- 1) As espécies respondem diferentemente à mudança climática através de seus atributos biológicos e ecológicos. Enquanto algumas espécies podem se beneficiar de um aumento de temperatura, outras podem ser severamente prejudicadas. A região geográfica e o grupo taxonômico são importantes determinantes da resposta das espécies. Isso torna a escolha das estratégias de conservação mais difícil e requer análises mais cuidadosas, uma vez que uma estratégia que deu certo para um determinado grupo de espécies em determinada região pode não ser adequada para outros grupos e outras regiões.
- 2) Além do monitoramento das populações de espécies mais vulneráveis, outras medidas de conservação como novas áreas protegidas, restauração e conectividade da paisagem também serão necessárias, uma vez que a distribuição das espécies mais vulneráveis está quase toda fora das áreas protegidas.
- 3) A maioria das populações das espécies de aves estarão expostas à altas mudanças no clima e perda da vegetação nativa em seus habitats. Como poucas áreas no Cerrado poderão servir como refúgios, muitas espécies terão que conseguir se adaptar a estas mudanças para evitar que ocorra uma redução na diversidade de aves no Cerrado.

- 4) A mudança climática e a mudança no uso da terra atuam de forma espacialmente opostas no Cerrado. Enquanto o clima afetará mais fortemente a região norte (que é a região que mantém a maior cobertura de vegetação nativa), a região sul (que é a região mais rica em espécies e que manterá condições climáticas mais adequadas) se encontra altamente desmatada e fragmentada. Como dificilmente conseguiremos interromper a mudança climática, estratégias de conservação como proteção dos habitats remanescentes, restauração de paisagens degradadas, implantação de corredores e trampolins ecológicos para manter a conectividade são extremamente importantes na região sul do Cerrado para a proteção das espécies de aves.
- 5) As mudanças climáticas e de uso da terra no Cerrado não afetarão apenas a diversidade de espécies, mas também as estruturas funcionais e filogenéticas das comunidades de aves. No futuro as comunidades se tornarão mais homogêneas funcionalmente e filogeneticamente, o que poderá afetar as funções ecossistêmicas e a história evolutiva das aves no Cerrado. Dada a incongruência espacial entre os três componentes da diversidade, uma abordagem integrada entre eles se torna essencial para superar o desafio de estabelecer estratégias de conservação que priorizam os diferentes aspectos da biodiversidade.