Universidade de Brasília

Instituto de Ciências Biológicas

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Resposta dos pequenos mamíferos do Cerrado à fragmentação e perda de habitat: uma perspectiva funcional e trófica

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> “*O saber se aprende com mestres e livros. A sabedoria, com o corriqueiro, com a vida e com os humildes.*”
>
> Cora Coralina

Tese de Doutorado

Ingrid de Mattos

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Sumário

Resumo

Há mais de 20 anos se iniciou um intenso debate sobre os efeitos relativos da perda de habitat e da fragmentação sobre a biodiversidade, frente ao avanço da destruição dos habitats e conversão da vegetação nativa em agricultura e pastagem. Uma conclusão geral é que a quantidade de habitat disponível é determinante para a persistência das espécies em uma paisagem modificada, e que as interações entre fragmento e matriz influenciam as consequências ecológicas dessas mudanças para as espécies. Porém, em paisagens com diferentes níveis de cobertura vegetal remanescente, o tamanho dos fragmentos e o isolamento entre eles podem ter efeitos variáveis sobre a biodiversidade, sendo potencialmente mais fortes em paisagens intermediárias.

Além disso, a degradação do habitat nos remanescentes resultante da conversão da paisagem pode contribuir para a perda de biodiversidade e para as mudanças na composição de espécies. Desta forma, processos ecológicos em diferentes escalas podem ocorrer simultaneamente, contribuindo para o desfecho do cenário de capacidade de sobrevivência das espécies nas paisagens fragmentadas. O conhecimento sobre essas questões pode contribuir significativamente para a eficácia das estratégias de manejo da paisagem aplicadas à conservação dos remanescentes nativos, das suas espécies habitantes e dos serviços ecossistêmicos prestados por elas. No cenário brasileiro, isso é de especial importância, pois a maior parte das áreas protegidas está localizada nas reservas legais e áreas de proteção permanente em áreas privadas.

A resposta das espécies a esses processos espaciais e locais depende de suas características relacionadas ao uso do habitat, tolerância à matriz, habilidade de dispersão, dieta e nível trófico. Assim, identificar o conjunto de características funcionais das espécies que estejam relacionadas à capacidade de persistência em paisagens modificadas é uma estratégia valiosa para se compreender as consequências ecológicas e funcionais das perturbações antrópicas nos ecossistemas. Afinal, os atributos funcionais representam componentes do fenótipo de um organismo que influenciam processos ecossistêmicos. Desta forma, para se compreender melhor a dinâmica e função das espécies e comunidades sobrevivendo em paisagens modificadas pelo homem, e suas relações com o funcionamento dos ecossistemas, é

importante caracterizar a biodiversidade em dimensões que vão além da clássica abordagem taxonômica, como é o caso das perspectivas funcional e trófica.

Neste contexto, esta tese visou investigar os efeitos relativos da perda de habitat, da fragmentação, e da qualidade dos remanescentes sobre diferentes aspectos da diversidade de pequenos mamíferos em áreas de floresta semidecídua no Cerrado, sob diferentes e complementares perspectivas (taxonômica, funcional e trófica). O trabalho está estruturado em três capítulos, e todos foram baseados em dados empíricos de captura dos animais realizados em 36 fragmentos florestais em áreas privadas no Estado de Goiás. Os remanescentes estiveram distribuídos em um gradiente de perda de habitat, estimado pela variação na proporção de cobertura vegetal nativa em uma escala de 15000 ha (10, 25 e 40%).

O primeiro capítulo teve por objetivo verificar como os padrões de abundância, riqueza e diversidade taxonômica e funcional das comunidades de mamíferos, assim como a composição de espécies, são influenciados pelo tamanho de fragmento, dependendo da proporção de habitat disponível na paisagem; ainda, foi também avaliado se a qualidade dos remanescentes (estimado como estrutura da vegetação) afeta esses parâmetros das comunidades. As capturas e a coleta de dados sobre a vegetação ocorreram durante quatro campanhas entre os anos de 2018 e 2019, nas estações seca e chuvosa. Os efeitos do tamanho dos fragmentos nas comunidades não dependeram da quantidade de habitat na paisagem. Porém, foi detectado um aumento da abundância geral das espécies em fragmentos menores, e um efeito negativo da quantidade de habitat na abundância apenas de espécies generalistas. Por outro lado, houve maior riqueza de generalistas em paisagens mais conservadas, enquanto a riqueza de especialistas foi influenciada pela qualidade do habitat nos fragmentos, mais especificamente, por florestas com dossel mais fechado. Com relação à composição de espécies, a estrutura da paisagem foi mais importante do que a qualidade dos fragmentos para explicar a variação na abundância das espécies entre as áreas. Como conclusão, parece haver um aumento geral da abundância das espécies com o aumento do nível de fragmentação e perda de habitat. Porém, a riqueza de espécies generalistas depende da maior disponibilidade de vegetação nativa na paisagem, enquanto o número de espécies especialistas responde a uma escala mais fina, e depende de florestas mais estruturadas, ou seja, da maior qualidade dos remanescentes.

Os dois capítulos seguintes abordaram diferentes aspectos das mudanças na ecologia trófica da espécie dominante na área de estudo, o marsupial didelfídeo *Gracilinanus agilis*, ao longo do gradiente de fragmentação e perda de habitat. Estas investigações se basearam no uso de isótopos estáveis de carbono (δ^{13}C) e nitrogênio (δ^{15}N), possibilitando inferir sobre a incorporação de recursos presentes na matriz de pastagem relativamente às florestas, e sobre mudanças no nível trófico. Os dados usados para esses capítulos se basearam nas amostras coletadas apenas no ano de 2018. O capítulo dois focou em compreender de forma geral como a fragmentação por si, dependendo do contexto da quantidade de habitat na paisagem, altera o tamanho do espaço de nicho trófico (uma métrica de diversidade trófica), e os valores isotópicos de carbono e nitrogênio da espécie modelo. Dentro de cada paisagem, os fragmentos foram elencados em três classes de tamanho (pequenos, médios e grandes), em que foram reunidas as amostras isotópicas para se gerar as elipses do nicho trófico. Não houve incorporação de recursos da matriz pelo marsupial em nenhuma situação. Por outro lado, houve mudança de nicho trófico na paisagem intermediária e na mais conservada: os animais transitaram entre maior grau de insetivoria para frugivoria de fragmentos pequenos para grandes, e este efeito foi mais forte quando houve mais floresta na paisagem. No contexto de maior perda de habitat, houve expansão do espaço de nicho trófico em fragmentos menores. Contrariamente, e progressivamente da paisagem intermediária para a mais conservada, o nicho se expandiu com o aumento do tamanho dos fragmentos. Os resultados demonstraram que *G. agilis* depende dos recursos alimentares da floresta presentes até nos menores fragmentos, e uma marcada mudança na sua ecologia trófica ao longo do gradiente de fragmentação, dependendo do contexto de perda de habitat. Isso indica que as alterações antrópicas na paisagem modificam a amplitude de nicho, a estrutura trófica e o papel ecológico da espécie.

Por fim, o terceiro capítulo consistiu em compreender a resposta trófica de *G. agilis* ao processo de fragmentação e perda de habitat, sob um enfoque mais local e adotando uma perspectiva em múltiplas escalas. Desta forma, investigou-se como a qualidade do habitat (avaliada como estrutura da floresta e disponibilidade de recursos), características do fragmento e da paisagem circundante (estimadas em um buffer de 1km ao redor dos remanescentes) determinam as métricas de espaço de nicho trófico da espécie. Neste capítulo, foram usadas amostras de cada fragmento para gerar as métricas de nicho isotópico. A amplitude do δ^{13}C não foi influenciada por nenhuma das escalas avaliadas, enquanto a amplitude de δ^{15}N respondeu à escala do fragmento, sendo positivamente influenciada pela quantidade de área core no fragmento, indicando que os indivíduos assimilaram maior diversidade de níveis tróficos em remanescentes maiores e mais conservados, em relação aos menores. A diversidade trófica

também não respondeu aos preditores avaliados em nenhuma escala. No entanto, a uniformidade de nicho respondeu a diferentes escalas: considerando a escala do habitat, houve maior convergência de nicho entre os indivíduos da mesma população em áreas com maior número de lianas e com maior abundância de térmitas; na escala do fragmento, o nicho dos indivíduos de uma população foi mais dissimilar com o aumento da área core do remanescente, ou seja, em fragmentos maiores e mais preservados. Os resultados mostram que diferentes aspectos da ecologia trófica da espécie respondem de formas distintas às diferentes escalas avaliadas, e que a resposta a nível do habitat e do fragmento prevaleceram sobre a escala da paisagem. Isso indica que a resposta às mudanças antrópicas para espécies de pequeno tamanho corporal pode se dar em escalas ambientais mais finas.

Palavras-chave: padrões de diversidade, ecologia trófica, degradação florestal, roedores e marsupiais, *Gracilinanus agilis*.

Abstract

It has been more than 20 years of debates on the relative effects of habitat amount and fragmentation on biodiversity, in face of the advance of habitat destruction and native cover conversion into agriculture and pastures. A general conclusion is that the proportion of remaining habitat is determinant for species persistence in modified landscapes, and that interactions between patches and matrix influence the ecological consequences of these changes for the species. However, in landscapes with different levels of remaining native cover, patch size and isolation may have variable effects on biodiversity, being potentially stronger in conditions of intermediate levels of habitat amount.

Moreover, the resulting habitat degradation from landscape conversion can contribute to biodiversity loss and for the changes in species composition. Therefore, ecological processes in different scales might occur simultaneously, contributing to the outcome of species capability to survive in fragmented landscapes. Knowledge on these issues may contribute significantly to the effectiveness of landscape management strategies applied to the conservation of remnants, of their inhabiting species and ecosystem services performed by them. In the Brazilian scenario, this is highly relevant, because most of the protected areas are in legal reserves and permanent protection areas inside private landholdings.

Species responses to these spatial and local processes depend on their characteristics related to habitat use, matrix tolerance, dispersal ability, diet, and trophic level. Thus, identifying the set of functional traits related to species capability to persist in modified landscapes is a valuable strategy to comprehend the ecological and functional consequences of human-driven disturbances in ecosystems. After all, functional traits represent phenotype components of an organism that influence ecosystem processes. In this sense, to better comprehend the dynamics and functions of species and communities surviving in human-modified landscapes, and their relationships with ecosystem function, it is important to characterize biodiversity in dimensions that go beyond the classical taxonomic approach, as it is the case of functional and trophic dimensions.

In this context, this work aimed at investigating the relative effects of habitat loss, fragmentation, and remnant quality on different aspects of the diversity of small mammals in semideciduous forests in the Cerrado, under different and complementary perspectives

(taxonomic, functional and trophic). The thesis is divided in three chapters, all of them were based on empiric data from animal captures carried in 36 forest patches in private landholdings in the state of Goiás. Remnants were distributed across a habitat loss gradient, estimated by the variation in the proportion of native cover in a scale of 15000 ha (10, 25 and 40%).

The first chapter verified how patterns of species abundance, richness and taxonomic/ functional diversity of mammal assemblages, as well as species composition, were influenced by patch size depending on landscape context of habitat amount; also, it was evaluated if patch quality (estimated as vegetation structure) affected these community parameters. Captures and data collection on vegetation occurred during four field phases between the years 2018 and 2019, in the dry and rainy season. The effects of patch size on assemblages did not depend habitat amount in the landscape. However, it was detected an increase of overall species abundance in smaller patches, and a negative effect of habitat amount in the abundance of generalist species. On the other hand, there was higher generalist richness in more conserved landscapes, while specialist´s richness was influenced by habitat quality inside patches, more specifically, by forests with higher canopy cover. Regarding species composition, landscape structure was more important than habitat quality to explain variations in species abundance between areas. As a conclusion, it seems to be a general increase of species abundance with the advance of fragmentation and habitat loss. However, the richness of generalists depends more on habitat availability in the landscape, while the number of specialists species responds to a finer scale, depending on more structured forests, e.g., of higher quality of remnants.

The two following chapters addressed different aspects of changes in the trophic ecology of the dominant species in the study, the didelphid marsupial *Gracilinanus agilis*, along the gradients of fragmentation and habitat loss. The research was based on the use of stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N), allowing inferences on the assimilation of matrix resources relatively to forests, and on trophic level shifts. These chapters were based on samples collected only in the year 2018. Chapter two focused on comprehending, as a whole, how fragmentation per se, depending on landscape context of habitat amount, alters the isotopic niche space (a metric of trophic diversity) and the isotopic values of carbon and nitrogen of the studied species. In each landscape, patches were classified according to size classes (small, medium, large), within which isotopic samples were reunited to generate the trophic niche ellipses. There was no incorporation of matrix resources by the marsupial in any situation. In contrast, there was a progressive niche shift from intermediate to more conserved landscapes,

where animals transited from insectivory to frugivory from small to large patches, and this effect was stronger with higher habitat amount. In the most eroded landscape, smaller patches showed a niche expansion. Results reveal that *G. agilis* depends on forest food resources even in the smaller patches and presents a marked change in trophic ecology along the gradient of fragmentation, depending on the context of habitat loss. It indicates that human-driven alterations in the landscape modify niche width, trophic structure, and the ecological role of the species.

Finally, the third chapter addressed the trophic response of *G. agilis* to fragmentation and habitat loss under a more local focus, adopting a multiscale approach. Therefore, it was asked how habitat quality (evaluated as forest structure and food availability), patch characteristics and surrounding landscape features (estimated in a 1km buffer around remnants) determined isotopic niche space metrics of the species. In this work, we used samples from each patch to estimate metrics. The δ^{13}C range was not influenced by any of the evaluated scales, while δ^{15}N range responded to patch scale, being positively influenced by patch core area, indicating that individuals assimilated more trophic levels in larger and more conserved remnants, relatively to smaller ones. Trophic diversity did not respond to the predictors at any scales. However, niche uniformity responded to different scales: considering the habitat, niche among individuals was more similar in populations from areas with higher numbers of lianas, and also in areas with more termites; at the patch scale, niche was more dissimilar with the increase of patch core area, i.e., in larger and more conserved patches. The results show that different aspects of the trophic ecology respond in distinct ways to the evaluated scales, and that the response at the habitat and patch level prevailed over the landscape scale. It indicates that the response of small-bodied species to human-driven changes might arise at finer environmental scales.

Keywords: diversity patterns, trophic ecology, forest degradation, rodents and marsupials, *Gracilinanus agilis.*

Capítulo 1

Effects of habitat loss, fragmentation, and habitat quality on small mammal assemblages in fragmented landscapes of a neotropical savanna

Abstract

Landscape conversion of natural environments into agriculture and pasture are driving to marked biodiversity declines in the tropics. Fragmentation effects might depend on habitat amount in the landscape, while habitat quality of remnants can also affect species but has been poorly studied relatively to spatial scales. Furthermore, the impacts of these human-driven alterations may go beyond species loss, possibly representing the loss of ecosystem functions and services. In this study, we investigated how changes in landscape configuration (patch size), habitat loss (considering a gradient of 10, 25 and 40% of remnant habitat amount), and habitat quality (forest structure) affect small mammal abundance, richness, taxonomic/ functional diversity and species composition in fragmented landscapes of semideciduous forests in the Brazilian Cerrado. We livetraped small mammals and measured habitat quality descriptors in 36 forest patches over the years 2018 and 2019 four times, encompassing the rainy and dry seasons, with a total capture effort of 45,120 trap-nights. Regression analyses indicated that the effect of landscape configuration was not depend on the proportion of habitat amount in the landscape to determine small mammal assemblages. However, both patch size and habitat loss impacted different aspects of assemblages and in distinct ways. Smaller patches were mainly linked to overall increase in small mammal abundance, while the abundance of generalists also was negatively affected by habitat amount. Generalist species richness was determined by the habitat amount in the landscape. Specialists´ richness was only influenced by forest quality inside patches, suggesting that species with higher habitat requirements might respond to finer-grain scales in respect of the consequences of fragmentation and habitat loss. Neither taxonomic or functional diversity were influenced by landscape structure or habitat quality. However, patch size and habitat amount in the landscape were the major drivers of changes in small mammal species composition relatively to habitat quality features in semideciduous forests in the Brazilian savanna.

Keywords: Cerrado, landscape structure, forest structure, rodents, marsupials, functional diversity

Introduction

Habitat loss and fragmentation are the main drivers to biodiversity declines on Earth (Pardini et al. 2010; Haddad et al. 2015; Hanski 2015; Laurance et al. 2018). In the tropics, these landscape alterations result mostly from the conversion of natural environments into agriculture and pasture (Fearnside 2001; Gibbs et al. 2010; Peres et al. 2010; Françoso et al. 2015; Strassburg et al. 2017). These human-driven changes may affect species abundance, richness and diversity (Andren 1994; Fahrig 2003; Laurance et al. 2011; Hanski 2015; Melo 2015; Bovendorp et al. 2019). Additionally, ecological traits might be filtered out and be replaced by homogeneous characteristics (Olden et al. 2004; Melo 2015; Almeida-Gomes et al. 2019), leading to deep changes in ecosystem functions and forest dynamics (see Laurence et al. 2000; Haddad et al. 2015; Laurance et al. 2018). Therefore, understanding not only the impacts of habitat conversion on taxonomic diversity, but also on functional diversity (i.e., the degree of functional differences among species in a community) (Petchey and Gaston 2006) allows a broader comprehension of the consequences of species loss in ecosystem processes, functioning and stability (Petchey and Gaston 2006). Thus, conservation strategies should be more effective in the goal of maintaining ecosystem services if they also consider the functional dimension of biodiversity (Cadotte et al. 2011; Freitas and Mantovani 2018).

Habitat amount in the landscape is an important determinant of species persistence in altered landscapes (Andren 1994; Fahrig 2003, 2013; Melo et al. 2017). However, fragmentation effects may vary depending on landscape context of habitat amount (Andren 1994; Pardini et al. 2010; Villard and Metzger 2014). In landscapes with high native cover, immigration among patches are elevated enough to maintain high overall species abundance and richness, because of proximity between fragments, irrespective to patch size (Pardini et al. 2010). As habitat loss advances, the relative importance of patch size and isolation to explain species loss and population declines increases (Andren 1994; Villard and Metzger 2014). Thus, the effects of landscape configuration to species richness and abundance should be evident when there are intermediate amounts of habitat in the landscape (Pardini et al. 2010; Martensen et al. 2012; Villard and Metzger 2014).

In severely eroded landscapes, though, connectivity is so jeopardized that metapopulations can no longer persist, due to high extinction and low colonization rates (Lande 1987; Andren 1994). Under this condition, even large patches could go through local extinctions because of stochastic events, being too isolated and vulnerable to additional loss of native cover at the landscape scale (With and King 1999; Fahrig 2003). Therefore, no relationship between species richness and patch size would be expected (Pardini et al. 2010).

Within these diverse spatial dynamics, the interactions between patch and matrix can influence the ecological consequences of landscape alterations for different species (Prevedello and Vieira 2010; Newmark et al. 2014; Wilson et al. 2016). Also, deterioration of patch habitat quality resulting from landscape conversion may contribute to species loss and changes in species composition (Tabarelli and Gascon 2005; Carrete et al. 2009; Delciellos et al. 2016; Zimbres et al. 2017; Hannibal et al. 2020). Despite the important role of habitat quality in regulating spatial dynamic in fragmented landscapes and influencing species distribution patterns, studies on this subject have been poorly investigated relatively to classical spatial approaches (Mortelliti et al. 2010). Moreover, the knowledge on this matter can improve considerably the effectiveness of management strategies applied to the conservation of remnants, their living species and the ecosystem services provided by them (Tabarelli and Gascon 2005). This is especially critical to Brazil´s environmental policies, because most of the protected areas in the country are in legally required forest set-asides in private landholdings (Galleti et al. 2010).

Non-flying small mammals (Rodentia and Didelphimorphia) are abundant, diverse, and perform key roles in ecosystems as seed/seedling predators, seed dispersers, prey for many predators and secondary consumers (Brown et al. 2001; Bisceglia et al. 2011; Ribeiro et al. 2019). Additionally, they respond to microhabitat structure (Kajin and Grelle 2012), resource diversity/availability (Previtali et al. 2009; Camargo et al. 2019), and are sensitive to environmental and landscape changes (Pardini et al. 2010; Melo et al. 2017; Hannibal et al. 2018). These characteristics make them potential indicators of environmental quality (Bonvicino et al. 2002) and an ideal group to access human-driven landscape impacts on biodiversity.

Here, we investigated how changes in landscape configuration (i.e., patch size), habitat loss (considering a gradient of 10, 25 and 40% of remnant habitat amount), and habitat quality (i.e., forest structure) affect small mammal abundance, richness, taxonomic/ functional diversity and species composition in fragmented landscapes of semideciduous forests in the Brazilian Cerrado. We expected the effect of patch size on community metrics to be dependent on landscape context of habitat amount. In landscapes with intermediate levels of habitat amount, patch size effects should be stronger especially for forest dependent species (Pardini et al. 2010; Villard and Metzger 2014; Melo 2015). Yet, in more degraded landscapes (10% of habitat amount) and in more conserved ones (40%), we expected to find no patch size effects on abundance, richness, and diversity, but only a positive effect of habitat amount. On the other hand, we predicted that generalist species should not respond to patch size, neither to habitat amount in the landscape, or would only present a patch size effect in the most degraded landscape (10%) (Pardini et al. 2010). Regarding habitat quality (here represented by forest structure features), we foresaw that more conserved patches (i.e., with more structured forests – higher complexity and heterogeneity) should harbor more species, in higher abundance, mainly for forest specialists. Therefore, assemblages in more complex forests should be more diverse in taxonomic and functional dimensions (Zimbres et al. 2017).

Also, we expected species composition to vary across the landscape structure gradient, also according to changes in habitat quality (i.e., forest structure). Rare species, forest specialists, with higher sensitiveness to environmental alterations would be more related to larger patches and/or landscapes with higher levels of habitat amount, as well as to more structured forests (Melo 2015; Hannibal et al. 2020). On the other hand, tolerant and generalist species would be more related to smaller patches, lower habitat amount in the landscape and low habitat quality (Melo 2015).

Materials and Methods

Study area

The study was conducted in remnants of semideciduous seasonal forests in three landscapes of ~15,000 ha with different levels of habitat amount (~ 10, 25, and 40 %) in a highly deforested portion in the Brazilian Cerrado. In each landscape we sampled 12 forest patches (totaling 36 sampling sites), ranging from 2 to 760 ha, where small mammals were surveyed. Sampling site choices were based on 1) the highest variation in patch size possible between those patches available in each landscape; 2) access easiness; 3) landowners' permissions. Sampling patches were located in the municipalities of Abadiânia (16º2´51´´ S 48º51´44´´ W), Jesúpolis (15°57´05´´ S 49°22´26´´ W), Jaraguá (15º44´31´´ S 49º20´6´´ W), Ouro Verde de Goiás (16°13´13´´ S 49°11´36´´ W), Pirenópolis (15°53´06.40´´ S 49°10´46.29´´ W), and São Francisco de Goiás (15º55´51´´ S 49º15´2´´ W), in the central portion of the state of Goiás, Brazil. In these regions, the matrix is comprised mainly of pasture, but there are also agricultural areas (such as crop fields and/or banana plantations) and few natural patches of savanna vegetation. Sampling sites were located in the Legal Reserves of private farms, which are the natural vegetation area all landowners are legally obliged to preserve. Also, there were 3 sites located in the surroundings of conservation units (Reserva Particular de Patrimonio Natural Vaga Fogo Farm, Pirenópolis – GO, and Parque Estadual da Serra de Jaraguá, Jaraguá – GO). The climate is classified as Aw according to Köppen, with two well defined climatic seasons (hot/wet summers from October to March, and dry/cold winters from April to September). To minimize differences in species composition between sampling sites, maximum distance between landscapes did not exceed 100 km and are located in the same river basin (Basin of Tocantins-Araguaia river).

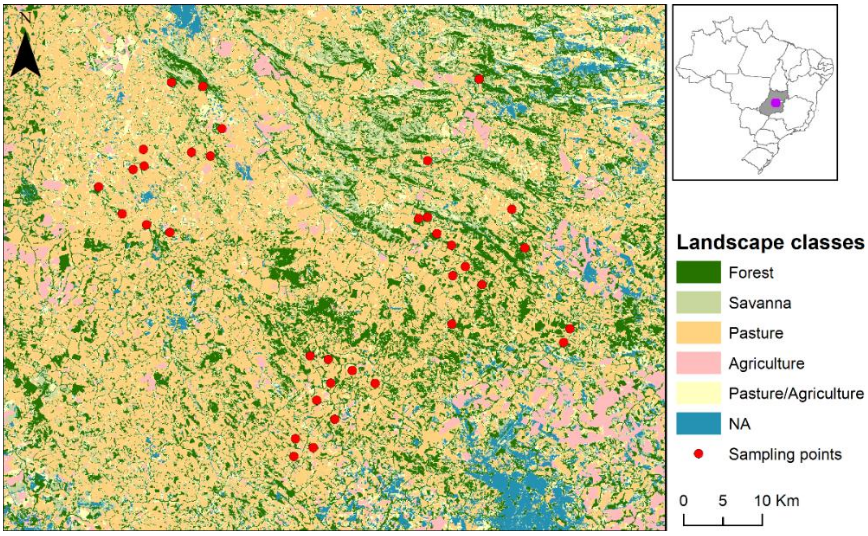

Figure 1. Landscapes of 15.000 ha with 10, 25 e 40% of habitat amount (including both forest and savanna), and the sampled patches (red dots) in central Goiás state, Brazil (highlighted in grey in the inset map). Patches located in the western portion of the map represent the landscape with 10% of remnant habitat amount, southern patches correspond to the landscape with 25%, and the eastern patches are in the landscape with 40% of habitat amount.

Small mammal survey

In each of the 36 sampled patches, we established a trapping line of 200 m, located 30 m from patch edges to minimize edge effects. Each line had 20 trap stations, placed every 10 m, with four livetraps each, where half were deployed on the ground, and half in the understory (at least

1.5 m height), totaling 80 traps per patch. Every station had a Tomahawk®(300 x 160 x 160 mm) and a small Sherman® (250 x 80 x 90 mm) on the ground, and a big Sherman (300 x 80 x 90 mm) and a small one in the understory, except for the first and last trap stations, where we replaced a Tomahawk trap by a big Sherman. The study was conducted over the years 2018 and 2019, in the following periods: rainy-dry season (April-June 2018), dry-rainy season (August-October 2018), rainy (February-April, and December 2019) and dry season (June-August 2019). Captures occurred for four consecutive nights per field campaign, resulting in an effort of 1,280 trap-nights per patch and 45,120 trap-nights in total.

Traps were baited with a mixture of peanut butter, corn powder, sardine, and banana. Captured animals were identified, marked with numbered ear-tags, measured and weighted. We also recorded age (following Macedo et al. 2006 for marsupials), gender, and reproductive status. Animals were released in the same trap location where they were captured. Voucher specimens were collected and will be held in the Mammal Collection of the Department of Zoology, University of Brasília (UnB, Brasília, Brazil). All procedures followed the guidelines of the American Society of Mammalogists for the use of wild animals in research (Sikes et al. 2016).

Landscape structure

We chose landscapes based on the 2016 land use and land cover map from the MapBiomas project, collection 4.0, which classifies Landsat 8 satellite imagery at a 30-m resolution. The temporal mismatch between the land cover map from MapBiomas and the field campaigns should be important since the study sites are within a relatively consolidated landscape in terms of human occupation. Landscape choice was based on the proportion of five land use classes: forest, savanna, agriculture, pasture, and mosaic of agriculture and pasture [see MapBiomas class description in (http://mapbiomas.org)].

Landscape structure was evaluated as patch size (ha) and proportion of habitat amount available in each landscape context [10, 25 and 40% of natural cover (forest plus savanna) as shown in Fig. 1]. These metrics were calculated using the Patch Analyst extension in ArcGis 10.2.

Habitat quality

Here we considered patch quality as properties of the habitat that might have an impact on population parameters such as survival and fecundity (Mortelliti et al. 2010). To evaluate habitat quality, we chose environmental variables revealed as important to small mammals´ occurrence and habitat use that can potentially affect population parameters and individual condition, therefore influencing species coexistence (Pardini et al. 2005; Ribeiro 2015a; Delciellos et al. 2016, 2018; Camargo et al. 2018; Hannibal et al. 2018, 2020). These variables describe habitat heterogeneity and forest complexity.

We sampled descriptors of habitat quality in ten 4 x 4-m plots located every even trap station along the transect line in all patches. To evaluate forest structure, we measured the following variables inside each plot: 1) canopy cover, as the proportion of closed pixels from a photograph (one per plot, and used mean values per patch) taken with a digital camera in the center of each plot, using the software image J. We took one picture per season and used mean values; 2) mean number of vines; 3) mean tree height (m) of the closest four trees from the plot center, with circumference ≥ 16 cm at 30 cm height - estimated with a 3 m pole; 4) basal area (m^2), estimated from the diameter at breast height (DBH) from the same four previously measured trees; 5) understory clutter (to 3 m height) (%), estimated with a graduated 3 m pole (with a graduation of 10 cm) following Martins et al. (2017); 6) litter volume (cm^3), estimated from litter material sampled in a 50 x 50-cm quadrat inside each plot (located in its superior left corner), following Santos Filho et al. (2008a). We placed the collected litter inside a translucid graduated cylindric box (with 28.2 cm diameter) and pressed down the material with a 1 kg cover, which indicated the correspondent litter height in a coupled scale of 120 mm (Figure 2). Litter height (h) was then used to estimate cylinder volume according to $V = \pi. (14.1)^2.h$.

Cattle ranching is the main human activity in study regions, so we also estimated 7) cattle intrusion to measure human-use habitat modification in forests. We classified intrusion level as an ordinated variable (0-4) based on incidence of footprints, cattle trampling and feces in a 15-m radius around each plot´s center. For this variable we used median plot values for each patch as the sample unit, while we used mean values for the other variables.

Figure 2. Graduated cylindric box used to estimate litter volume.

Functional traits

To access species functional responses to habitat loss and fragmentation, as well as to habitat quality, we used morphological and behavior traits related to habitat use and trophic habits, which might influence species tolerances to landscape alterations (Table AI). We measured the following quantitative morphological traits in the field: 1) Tail length (mean tail length/ mean body length), which is related to vertical use of space: longer tails are associated to more arboreal habits (Eisenberg and Wilson 1981); 2) Hind feet width (mean width/mean length of hind feet), which is related to locomotion habits, thus, to use of space: short and wider hind feet are associated to more arboreal habits, while longer and straight hind feet indicate more cursorial habits (Camargo et al. 2008; Vieira and Camargo 2012); 3) Body weight (g), a feature related to food resource use (influencing prey size consumed), metabolic costs (MacMillen 1983), travel speed (Hirt et al. 2017), dispersal distance (Whitmee and Orme 2013), trophic niche partitioning (Andreas et al. 2013), foraging behavior and predation risk (Kotler and Brown 1988); 4) Arboreality index (number of captures in understory/total number of captures) which measures the use of vertical space by species (Camargo et al. 2019b). As categorial variables, we classified species based on information available in the literature according to: 5) habitat specificity (forest specialists – species restricted to forested environments, or generalists – species that inhabits forests as well as open areas, grasslands, savannas, crop fields) (Tab. AI); and finally the multichoice binary variable 6) Diet – representing a combination of the following trophic guilds: insectivore, frugivore, granivore (that feeds on seeds or grains) and omnivore (Paglia et al. 2012; Shiels et al. 2014; Riofrío-Lazo and Páez-Rosas 2015).

Data analyses

Community metrics

We evaluated species richness [with Chao1 estimator (Colwell et al. 2012)], and abundance (as the total number of individuals captured in each patch) separately for forest specialists and generalists. Considering species altogether, we estimated taxonomic species diversity with true diversity Shannon Index (exp(H´)) (Jost 2006), and functional diversity (FD) was evaluated as the as Rao´s quadratic entropy (Q). It measures functional distance between pairs of individuals and incorporates species abundances (Botta-Dukát 2005), besides being weakly influenced by species richness (Laliberté and Legendre 2010; Pavoine and Bonsall 2011; Dias et al. 2013).

We used Gower distance to estimate FD, since we had continuous, categorical, and binary traits (Podani and Schmera 2006; de Bello et al. 2010). Taxonomic metrics were calculated in *vegan* R package (Oksanen et al. 2019), while functional diversity was estimated with package *FD* (Laliberté et al. 2015).

Community metrics and the effects of fragmentation and habitat loss

To evaluate the relative effects of patch size according to landscape context of habitat amount, we performed regression analyses with generalized linear models (GLM) with lme4 package (Bates et al. 2015). GLM were used to accommodate residual deviations from normality. Also, according to the response variables evaluated and models´ residual dispersion, we used different distribution families (Gaussian, Gamma, Poisson, Negative Binomial, Table AII) (Zuur et al. 2009). To determine which variables were most important to influence response variables, nested models were compared by likelihood ratio tests (LRT). The significance of explanatory variables was given by Deviance and p-values (based on χ^2 test). For all global models, we investigated spatial autocorrelation in model residuals with Moran´s I associated with bubble plots from *sp* package in R (Pebesma and Bivand 2005). Also, we checked for multicollinearity between predictors with variance inflation factor (VIF) in all global models (Zuur et al. 2007). During model fitting, we transformed patch size to log (x) to improve homoscedasticity of residuals (Zuur et al. 2007). Moreover, predictors were standardized (scaled to the z-score) to ensure variables had the same scale. We tested for overdispersion with Pearson residuals in all global models and used Negative Binomial GLM to correct it whenever needed. We performed model validation following Zuur et al. (2009).

Community metrics and habitat quality

We evaluated the effects of habitat quality features in community metrics following the same protocol described above for GLM. However, first we performed a principal component analysis (PCA) to reduce data dimensionality of forest structure variables (Borcard et al. 2011). Thus, we used scores from PC1 and PC2 (summarizing >50% of variables variation between sampling sites) as predictors in GLM models. Before running the PCA, we checked for multicollinearity between habitat variables and excluded those with Pearson correlations > 0.5, and scaled variables to the z-score.

Species composition, landscape structure and habitat quality

To evaluate if changes in species composition were explained by the fragmentation and habitat loss gradients, as well as by habitat quality features, we applied a redundancy analysis (RDA) with *vegan* package (Oksanen et al. 2019). We used species abundance matrix with Hellinger transformation (Borcard et al. 2011) as the response variable, while patch size, proportion of habitat amount in the landscape and PC1 and PC2 were inserted as scaled predictors. Moreover, global significance of RDA model, significance of RDA axis and significance of model terms (predictors) were tested with permutation tests with 1000 randomizations (Borcard et al. 2011). Before running the model, we tested for spatial autocorrelation between species composition and geographic coordinates with Mantel correlograms with 999 randomizations.

All analyses were conducted in R version 3.6.2 (R Core Team 2019).

Results

With a capture success of 4.56%, we captured 1323 individuals, recaptured 735 times, belonging to 15 species, five marsupial and 11 rodent species (Table 1). Most abundant species in the study were the marsupials *Gracilinanus agilis* (n = 840 individuals, 63% of total captures) and *Didelphis albiventris* (n=134, 10%), followed by the rodents *Oecomys cleberi* (n=121, 9.1%) and *Rhipidomys macrurus* (n=70, 5.2%) (Tab. 2). Rarest species were the exotic european rodent *Rattus rattus* (n=1) and *Oligoryzomys nigripes* (n=1). Landscape with intermediate habitat amount (25%) showed higher abundance and observed richness (Tab. 1).

Regression models were not overdispersed, and most of them presented no spatial autocorrelation according to Moran´s I test (Table AII). However, whenever we detected spatial autocorrelation in model residuals, the visual inspection of residuals dispersion (Zuur et al. 2009), associated with the visualization of bubble plots of the model´s Pearson residuals and site coordinates (i.e., no clear spatial pattern detected, overall small correlation values and only a few sites presenting higher values), led us to conclude that correlations were not linked directly to the spatial variation of measured variables themselves, thus being considered second order correlations (stochastic or purely random). In this sense, we did not consider them strong enough to invalidate the global model, so we proceeded the analyses (Figures AI, AII, AIII, AVI, AVII, AVIII).

Community metrics and the effects of fragmentation and habitat loss

Regarding generalists species abundance, we found a strong negative effect of patch area ($\beta_{\text{log (patch area)}}$ = -0.44 ± 0.09; df = 33; p = 1.022 x 10^{-5}, Table AII, Figure 3a) and a slighter significant negative effect of habitat amount in the landscape ($\beta_{\text{landscape}}$ = -0.24 ± 0.09; df = 33; p = 0.019, Tab. AII, Fig. 3b). In other words, generalist species were more abundant in smaller patches and in landscapes with lower proportion of habitat amount. For specialists´ abundance, GLM revealed only a negative effect of patch area irrespective to landscape habitat amount ($\beta_{\text{log (patch area)}}$ = -0.47 ± 0.19; df = 34; p = 0.007, Fig.3c).

In relation to estimated species richness, we found a positive effect of landscape habitat amount for generalists, indicating more conserved landscapes presented more species regardless of patch size ($\beta_{\text{landscape}}$ = -0.047 ± 0.02; df = 34; p = 0.043, Tab. AII, Fig. 3d). For specialists, we failed to detect any effect of landscape structure in estimated species richness (Tab. AII).

Moreover, regression models indicated that variations in species diversity neither in functional diversity were explained by landscape structure (Tab. AII).

Community metrics and habitat quality

Considering forest structure, here used as habitat quality features, the only variable excluded from the data set used in PCA analyses because of multicollinearity was level of cattle intrusion, since it was highly correlated with understory clutter (r = -0.75, Figure AIV). The first component of PCA explained 29.55% of data variation, while the second explained 23.45%. PC1 was more related to basal area and tree height (loading values ≥ 0.5), whilst PC2 was more loaded by canopy cover (Table AIII). So, PC1 axis represented, from negative to positive values, a gradient of sites with shorter trees and lower basal area towards patches with taller and larger diameter trees. On the other hand, from negative to positive values, PC2 denoted a gradient of more open to more closed-canopy forests.

Among all community metrics evaluated (abundance of generalist and specialist species, estimated richness for generalist and specialist species, species diversity and FD), we only detected an effect of habitat quality for the estimated richness of forest specialists. Specialists numbers were positively associated with PC2 axis, indicating that patches with higher canopy cover harbored more specialist species (β_{PC2}= 0.25± 0.10; df = 34; p = 0.018, Tab. AIV, Fig. 4).

Table 2. Small mammal abundance matrix and number of species registered in semideciduous forest patches (sampling sites) distributed in the landscapes representing a gradient of fragmentation and habitat loss in central Goiás between 2018 and 2019.

	40%												**25%**												**10%**												
Species	**F2**	**F3**	**F4**	**F5**	**F6**	**F7**	**F8**	**F9**	**F10**	**F14**	**VF**	**M**	**F15**	**F16**	**F17**	**F18**	**F19**	**F20**	**F21**	**F22**	**F23**	**F24**	**R1**	**R2**	**F25**	**F26**	**F27**	**F28**	**F29**	**F30**	**F31**	**F32**	**F33**	**F34**	**PSJ1**	**PSJ2**	**Total**
Calomys expulsus	0	0	0	2	0	0	2	6	0	1	0	0	1	1	1	0	2	0	1	4	1	0	4	0	1	5	8	7	6	0	1	6	3	0	0	1	64
Calomys tener	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	2	1	2	0	4	0	0	0	2	0	0	0	14
Cryptonanus agricolai	0	0	0	3	0	0	0	0	1	0	0	0	0	8	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	1	0	1	1	2	0	2	24
Didelphis albiventris	0	14	3	1	1	4	5	5	5	3	1	1	13	1	0	2	1	12	13	15	3	5	1	5	0	1	0	0	0	6	1	2	3	3	3	1	134
Gracilinanus agilis	2	14	61	19	3	12	21	35	6	8	1	7	33	43	12	34	45	1	63	52	20	10	21	18	14	17	25	41	24	49	12	29	26	38	18	6	840
Hylaeamys megacephalus	0	3	1	0	0	2	0	0	0	0	0	0	0	0	1	4	1	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15
Marmosa demerarae	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	8
Marmosa murina	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8
Oecomys catherinae	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	1	0	0	0	8
Oecomys cleberi	3	2	2	0	0	0	0	3	0	0	1	0	0	5	1	1	12	1	7	6	0	12	0	0	0	1	1	0	12	2	17	4	0	21	6	1	121
Oligoryzomys mattogrossae	0	0	0	3	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
Oligoryzomys cf. moojeni	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
Oligoryzomys nigripes	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Rhipidomys macrurus	0	0	20	0	0	0	3	0	0	0	0	0	6	24	0	0	1	0	2	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	70
Rattus rattus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Total abundance	304												567												452												
	5	41	87	28	8	18	31	49	12	12	5	8	54	84	15	43	66	16	86	92	29	32	27	23	18	27	36	48	49	59	31	42	36	64	27	15	1323
Observed richness	11												12												10												
	2	6	5	5	4	3	4	4	3	3	4	2	5	8	4	6	8	4	5	6	6	5	4	2	4	7	4	2	5	5	4	5	6	4	3	7	15

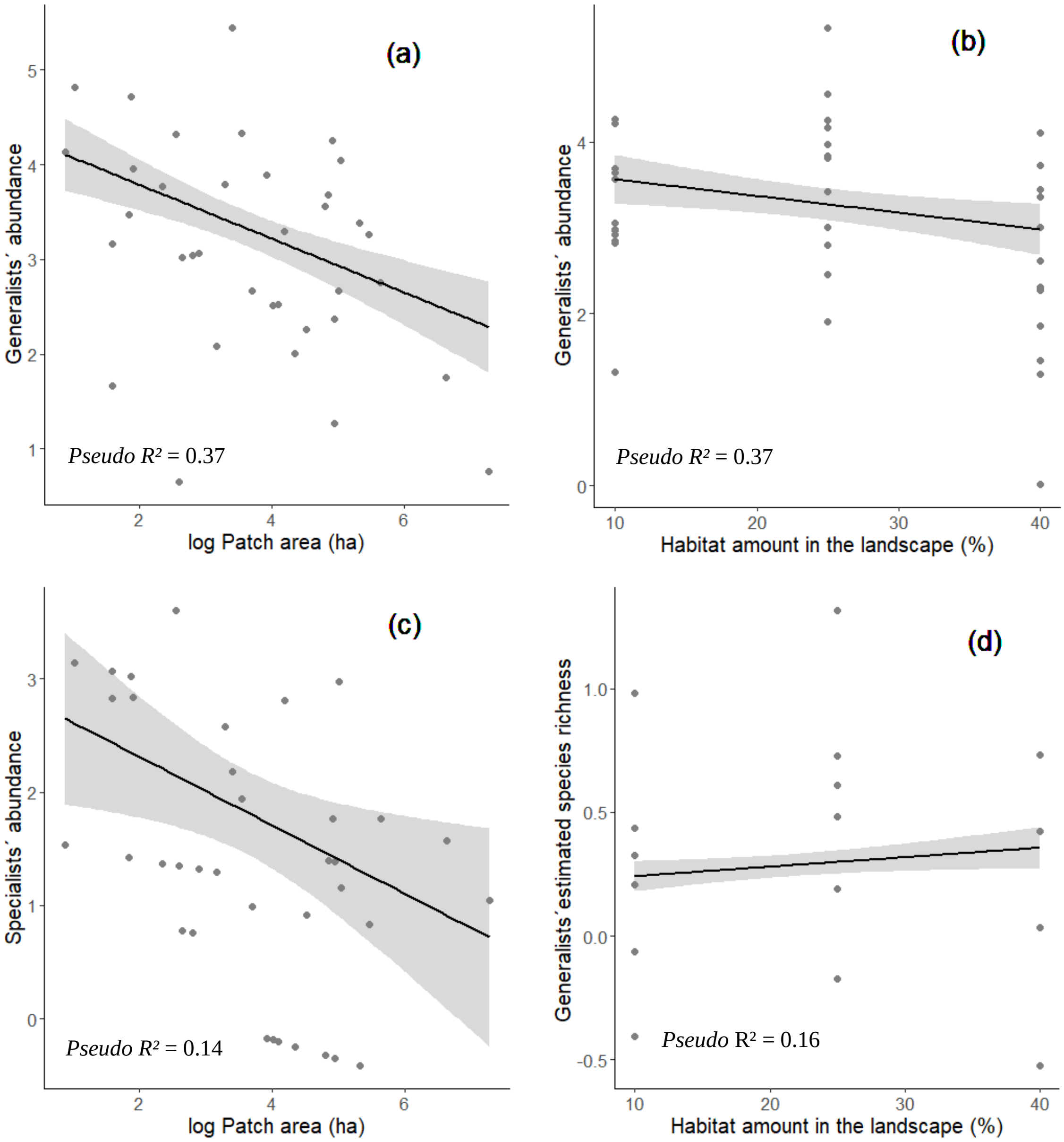

Figure 3. Final regression models revealing the effects of landscape structure in small mammal community metrics in semideciduous forest patches in central Goiás in the Brazilian Cerrado, including: patch area (a) and proportion of habitat amount in the landscape (b) for the abundance of habitat generalists; the effect of patch area (c) for forest specialists and an effect of proportion of habitat amount in the landscape (d) for generalist´s estimated species richness (Chao 1).

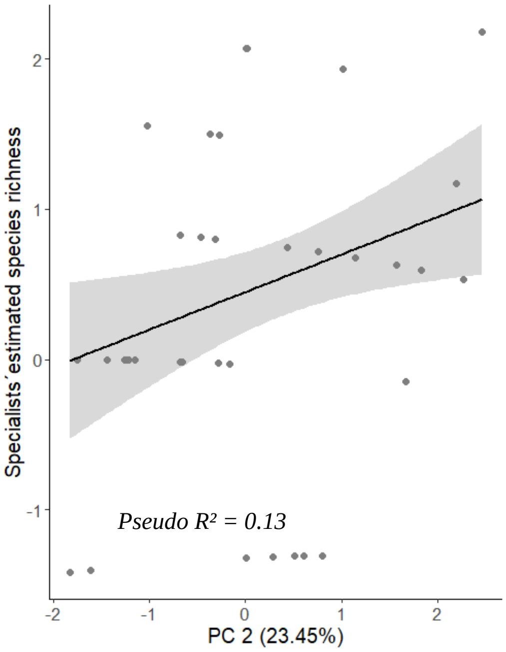

Figure 4. Final regression model revealing the effect of habitat quality in small mammal estimated species richness for forest specialists (by Chao 1 estimator) in semideciduous forest patches in central Goiás in the Brazilian Cerrado. PC 2 corresponds to the second axis of a principal component analysis of six forest structure variables used to describe habitat quality.

Species composition, landscape structure and habitat quality

We found no spatial autocorrelation between species composition and geographic coordinates of sites (Figure AIV). The RDA representing the relationship between species composition, landscape structure and habitat quality explained 10% of the variation of species abundance across sites (*adjusted* R^2 = 0.10; p = 0.009). In total, the first two axis explained 85% of data variation (RDA1 explained 50% and RDA2, 35%). However, only RDA1 axis was significant (p = 0.009), and among the explanatory variables, only patch area (p = 0.006) and landscape (p = 0.007) were significant.

Evaluating the RDA triplot (Figure 5) together with significances of axis and predictors, we observed that both evaluated landscape structure variables (looking at RDA1, longer blue arrows with greater projections in this axis) were much more important to explain the variation in species composition in sampling sites than the habitat quality features. From negative to positive values in RDA1, a clear gradient of patch size and habitat amount emerged: larger patches, inserted in landscapes with higher amount of habitat (left side of the triplot), towards smaller patches located in more degraded landscapes (right side of the triplot). Additionally, we could also observe that there were species clearly correlated with these explanatory variables (indicated by longer red arrows with greater right angled projections in the RDA1 axis): *Didelphis* was considerably associated with higher amounts of forest cover in the landscape, regardless of patch size, while the marsupial *M. demerarae* was very associated with larger patches, despite of forest cover in the landscape. On the other hand, *G. agilis* showed great association with smaller patches, independently of habitat amount. The generalist rodents *C. expulsus* and *C. tener* were very associated with more deforested landscapes but were not related to patch size. *Oecomys cleberi* was moderately related to patch size and to a greater extent, to less habitat amount in the landscape. The other species bunched together away from the extremes apparently are not influenced by the evaluated predictors.

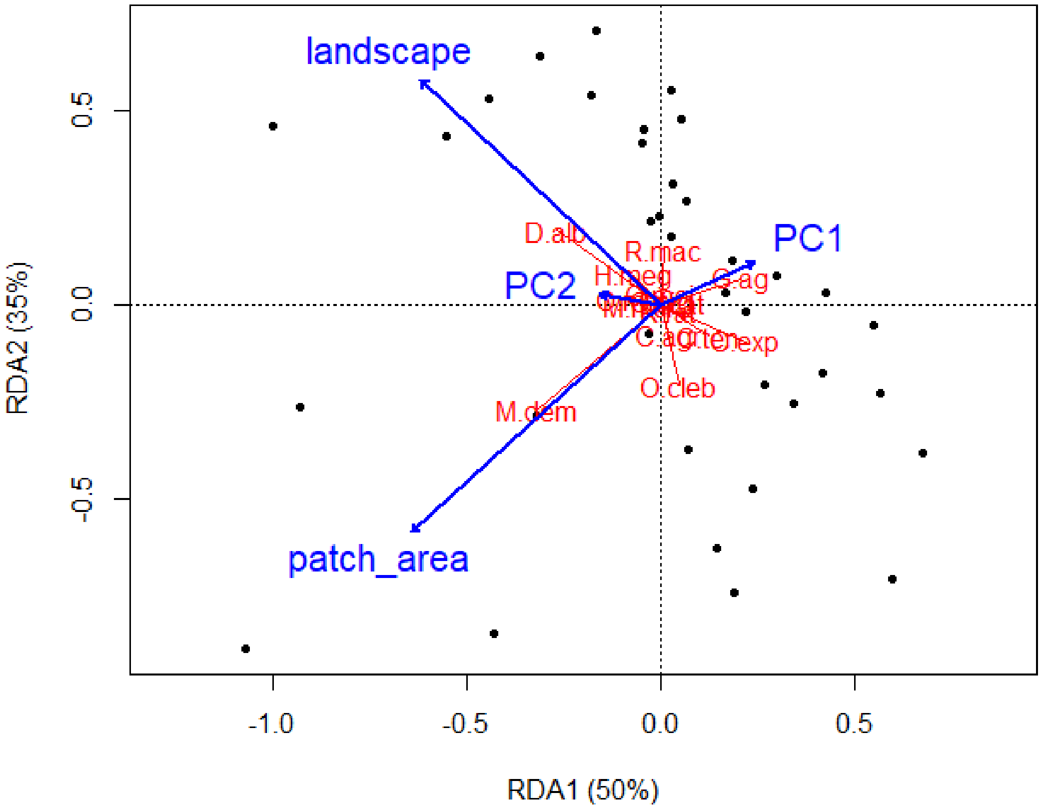

Figure 5. RDA triplot (Scaling 2 method – correlation plot) showing the relationship between small mammal species composition, landscape structure [patch area (patch_area) and proportion of habitat amount in the landscape (landscape)] and habitat

quality (PC1 and PC2 correspond to the first and second axis of a principal component analysis of six forest structure variables used to describe habitat quality) in semideciduous forest patches in the Brazilian Cerrado in central Goiás. Species are shown in red: *Calomys expulsus* (C.exp), *C. tener* (C.ten), *Cryptonanus agricolai* (C.agr), *Didelphis albiventris* (D.alb), *Gracilinanus agilis* (G.ag), *Hylaeamys megacephalus* (H.mega), *Marmosa demerarae* (M.dem), *M. murina* (M.mur), *Oecomys catherinae* (O.cat), *O. cleberi* (O.cleb), *Oligoryzomys mattogrossae* (O.mat), *O. moojeni* (O.mooj), *O. nigripes* (O.nig), *Rattus rattus* (R.rat), *Rhipidomys macrurus* (R.mac). Sampling sites are represented by black dots.

Discussion

In face of the actual high rates of deforestation and conversion of natural landscapes of the Brazilian Cerrado into croplands and pastures, associated with low protection legislation (Fearnside 2001; Strassburg et al. 2017), it is essential to better comprehend the impacts of fragmentation and habitat loss for species in order to properly address effective policies for conservation priorities and restauration plans for remnants of the world´s richest savanna (Faleiro et al. 2013).

Contrary to our expectations, we did not find any patch size effects depending on landscape context of habitat amount on abundance, richness, taxonomic and functional diversity, independently of species level of habitat specificity. However, generalists and specialists responded differently to the isolated effects of landscape structure features, while only specialist richness was affected by habitat quality. Furthermore, small mammal diversity metrics did not respond to either landscape structure or habitat quality.

Contradicting our hypothesis, the abundance of generalist and specialist species responded negatively to patch size, indicating that smaller patches held higher overall small mammal abundance. However, only generalists responded to the proportion of habitat amount in the landscape, being more abundant in more deforested landscapes, according to the findings of Pardini et al. (2010) for generalists in the Atlantic Forest. In addition, the same pattern for generalists was also found by Melo (2015) in woodland savannas in Mato Grosso state. However, for specialists´ abundance, she only found a negative effect of patch size in intermediate landscapes (30% of habitat amount), while specialists were more abundant according to higher forest cover in the landscape. In the

Amazon Forest, an increase of small mammal abundance with the reduction of forest area was also registered (Palmeirim et al. 2020).

The overall increase in species abundances (for generalists and forest specialists) that we found in smaller patches might be linked to several ecological processes. First, at some extent, we believe that there might be an ecological release from predators like medium-sized mammals, raptors, owls and snakes, since these are important predators to small mammals and can suffer negatively with fragmentation and habitat loss (Carrete et al. 2009; Fenker et al. 2014; Rocha et al. 2018). Additionally, there might be an ongoing competition release effect because of defaunation of large seed-predator mammals (Dirzo et al. 2014; Galetti et al. 2015a). It has been observed that defaunated forests lead to the increase in the abundance of small seed-predators, specially rodents (Galetti et al. 2015b). Moreover, but to a lesser extent, forest invasion by matrix tolerant species (for example, *Calomys* species) can contribute to the increase of the abundance of generalists in smaller fragments and in more eroded landscapes, which is probably linked to higher edge effects (Pardini 2004; Santos-Filho et al. 2008). Also, in our study, major increase in generalists´abundance, mainly in smaller patches, should be an effect of higher abundance of the dominant species *Gracilinanus agilis,* that represented almost 64% of all captures.

Finding no patch size effects either for specialist or generalist species richness, but identifying a habitat amount effect (even though only for generalist species) suggests that landscape vegetation cover is a better predictor of species richness than patch size, as proposed by Fahrig (2013) in the "*Habitat Amount Hypothesis*" and later confirmed by Melo et al. (2017) for overall small mammal species richness in woodland savannas in the Brazilian Cerrado, as well as for other animal groups (Garmendia et al. 2013; Ikin et al. 2014; Arroyo-Rodríguez et al. 2016). Landscape scale responses might variate among ecosystems, with species level of habitat specificity (Pardini et al. 2010; Melo 2015) and also with matrix habitat quality, an important feature of landscape-mediated processes that can severely impact animal movements across the landscape and influence colonization/extinction rates among patches (Palmeirim et al. 2020).

In fragmented landscapes, higher amounts of habitat should reduce overall patch isolation (Pardini et al. 2010), thus increasing inter-patch connectivity and favoring movements of certain species between patches (Vieira et al. 2009). Within this dynamic, matrix type and finer-scale matrix elements such as scattered trees should play an important role on which species can be well succeeded in inter-patch movements (Prevedello and Vieira 2010; Garmendia et al. 2013; Muanis 2017). Structurally simplified matrix areas, such as the dominant pasture matrix in our study, might be more impermeable for forest specialist species than for habitat generalists, since matrix type effects depend on species-specific habitat requirements, and matrix quality for organisms is linked to patch structure similarity (Prevedello and Vieira 2010; Arroyo-Rodríguez et al. 2016). In this sense, our findings on the relationship between generalist species richness and habitat amount should be expected. Moreover, the lack of a habitat amount effect for specialists, opposing the results of other studies (Pardini et al. 2010; Melo 2015), also indicates that in our study system there might be more important factors influencing species richness than spatial scales.

In altered landscapes, habitat conditions inside patches (i.e., patch quality) might be equally or more important than spatial scales to determine assemblages (Ikin et al. 2014; Delciellos et al. 2016; Zimbres et al. 2017; Palmeirim et al. 2020), since habitat features may be more related to the proximate effects of fragmentation consequences in ecosystems for species (Ikin et al. 2014). Thus, habitat degradation resulting from fragmentation processes can impair species persistence in fragments, reducing species richness, specially forest specialists (Zimbres et al. 2017).

Indeed, in our study, habitat quality features predicted specialist´s richness, indicating that forests with higher canopy cover harbored more species. A more closed canopy cover suggests higher levels of forest integrity, or more structured forests. Fragmentation leads to tree mortality of large trees (as a consequence of vulnerability to increased desiccation from edge effects exposure, associated to secondary causes such as fires and logging activities), which can reduce the canopy cover and the presence of emergent species, diminishing forest volume and structural complexity (Laurence et al. 2000). Environmental complexity offers more opportunities for species coexistence, leading to vertical niche stratification of small mammals, thus increasing species turnover between forest strata, and consequently enhancing richness (Camargo et al. 2018). Our findings reinforce the relative importance of the role of patch forest quality compared to spatial scales for maintaining specialist species, that require more complex forests to persist in a fragmented landscape.

Contrary to our expectations, we failed to detect any effects of landscape structure or habitat quality characteristics in patterns of taxonomic or functional diversity.

Responses of animal diversity patterns to landscape structure are rather idiosyncratic: several studies identified positive patch size effects not only for small mammal taxonomic (Melo 2015; Bovendorp et al. 2019) and functional diversity (Melo 2015; Zimbres et al. 2017; Bovendorp et al. 2019), while others also failed to find these effects on the evaluated diversity dimensions (Palmeirim et al. 2020; Sancha et al. 2020; Smith et al. 2020); in the same way, forest cover (i.e., habitat amount in the landscape) did not affect functional diversity of Atlantic forest small mammals (Sancha et al. 2020), while it was an important predictor for forest-dependent frog species in the same biome (Almeida-Gomes et al. 2019). Bovendorp et al. (2019) suggested that besides species-area effects, ecological interactions of predation or competition represented by the occurrence of medium and large sized mammals should contribute to the retention of species and functional diversity of small mammal communities in the Atlantic Forest. On the other hand, small mammal functional diversity might be better predicted by temperature variables, rather than landscape structure (Sancha et al. 2020).

Finally, several studies show that small mammal species composition has been strongly influenced by fragmentation and habitat loss, leading to markedly species turnover with the reduction of specialist species and increased dominance of generalist species (Vieira et al. 2009; Pardini et al. 2010; Banks-leite et al. 2012; Garmendia et al. 2013; Melo 2015; Palmeirim et al. 2020). Also, habitat quality inside patches related to landscape alterations have been also indicated as important determinants of changes in species composition (Melo 2015; Delciellos et al. 2016; Hannibal et al. 2018, 2020). However, our results show that landscape structure variables (patch size and proportion of habitat amount in the landscape) were the major drivers of changes in small mammal species composition relatively to habitat quality features in semideciduous forests in the Brazilian savanna.

Surprisingly, *D. albiventris* was the only species markedly associated with higher amounts of forest cover in the landscape. Even though the genus *Didelphis* is considered a habitat generalist with the ability to occupy even urban areas (Cáceres 2000; Wright et al. 2012), apparently it also depends on higher forest cover at the patch (Santos-Filho et al. 2008) or landscape scale. In addition, *D. marsupialis* showed declining occupancy probability in more degraded forests in the Amazon Forest (Zimbres 2016). These results suggest that even common and generalist species might have minimum habitat requirements to persist in human-modified landscapes.

Marmosa demerarae, one of the rarest species of our study, on the other hand, was related to large patches, irrespective to the surrounding proportion of habitat amount. In the Atlantic Forest it was associated with forest edges and to second growth forest matrix (Pardini 2004), and reproductive males were able to travel among patches across a matrix composed by tall grasses, shrubs and scattered trees (Pires et al. 2002). However, Santos-Filho et al. (2008) registered high abundance of this species in the interior of forest patches, nevertheless it was never captured in the pasture matrix. Despite these variations in abundance and responses to edge effects and matrix permeability found in other studies, our results indicated that *M. demerarae* is a sensitive species to fragmentation in the Brazilian Cerrado, and this sensitiveness might be affected by the quality of the surrounding matrix.

Conversely, *G.agilis*, the dominant species of our study, was strongly associated with smaller patches, independently of landscape vegetation cover. This abundant and generalist species has been indicated to be less susceptible to habitat fragmentation, not suffering from edge effects (Santos-Filho et al. 2008) and responding negatively to patch size (Cáceres et al. 2010). Also, it has been positively associated with the number of lianas, a proxy for forest disturbance (Campbell et al. 2015; Hannibal et al. 2018).

The rodents *C. expulsus* and *C. tener* were more associated with deforested landscapes but were not influenced by patch size. In the Cerrado, the genus *Calomys* are common inhabitants of open areas such as grasslands and savannas (Marinho-Filho et al. 2002). However, they can also be equally present in edges and inside forest patches in fragmented landscapes, as well as in the pasture matrix (Santos-Filho et al. 2008). They have been positively associated with environmental disturbances such as fire (Vieira 1999), also with lower forest NDVI, indicating a relationship with lower levels of forest integrity (Hannibal et al. 2018).

Lastly, *Oecomys cleberi* was moderately related to the increase in patch size and to forest cover in the landscape. Thus, this species might be sensitive to small patches but may tolerate some level of forest disturbance at larger scales. In fact, *Oecomys* genus apparently are less affected by edge effects (Santos-Filho et al. 2008), however are not able to use pasture matrix, which might represent a barrier to dispersal and a condition of dependency on resources available inside resident patches. Additionally, the congener *O. bicolor* was positively related to canopy cover and to NDVI (Hannibal et al. 2018) in semideciduous forests in the Cerrado, indicating demands for better conditions of forest structure, which is usually not the case of smaller patches (Laurence et al. 2000).

Contradicting our expectations, the results of this work indicated that the effect of landscape configuration did not depend on the proportion of habitat amount in the landscape to determine small mammal assemblages, as found in other studies in the Brazilian Cerrado (Melo 2015) and in the Atlantic Forest (Pardini et al. 2010). However, both landscape structure characteristics impact different aspects of assemblages and in distinct ways. Patch size was mainly linked to overall increase in small mammal abundance, while generalist species richness was determined by the habitat amount in the landscape. This result reinforces that habitat amount should be a better predictor of species richness than patch size, as proposed by (Fahrig 2013) and Melo et al. (2017). On the other hand, specialists´ richness was only influenced by forest quality inside patches, suggesting that species with higher habitat requirements might respond to finer-grain scales in respect of the consequences of fragmentation and habitat loss. In this sense, our study demonstrates the importance to include habitat quality changes as issues to be addressed in landscape research (Delciellos et al. 2016), in order to better understand the consequences of fragmentation and habitat loss in ecosystems, which depend on species characteristics and their habitat requirements. Lastly, we failed to detect any effects of either landscape structure or habitat quality in diversity dimensions.

We propose that future studies on the consequences of fragmentation and habitat loss to small mammals investigate the impacts of species interactions (predators and competitors) in community dynamics, since defaunation apparently is a strong driver of changes in abundance and diversity dimensions of small mammals in altered landscapes (Galetti et al. 2015b; Bovendorp et al. 2019) and has profound consequences to ecosystems (Dirzo et al. 2014; Soares et al. 2015; Marjakangas et al. 2020). Furthermore, we also suggest researchers to evaluate the effects of matrix structure and quality in the studies to better understand the broader responses of species surviving in fragmented landscapes. These knowledges are essential to support more effective conservation plans and actions in landscape management policies.

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Appendix I

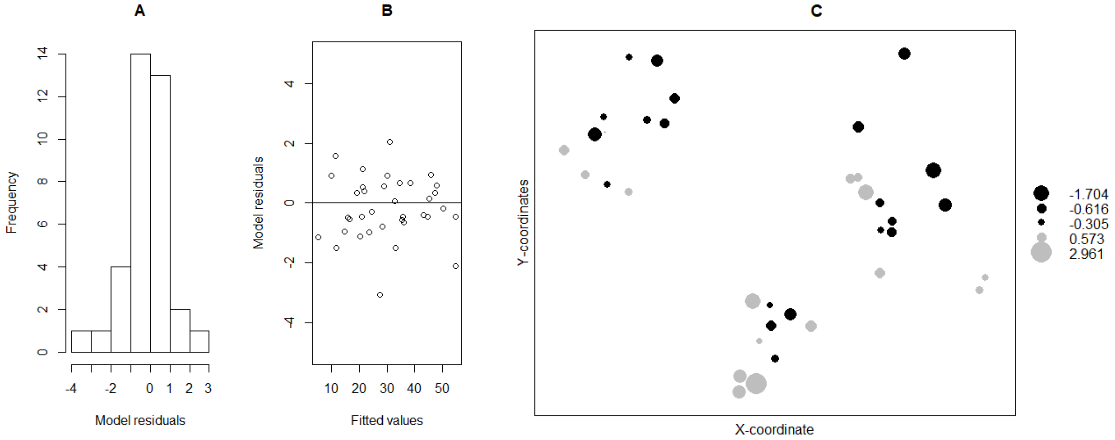

Figure AI. Model assumptions of normality (A), homogeneity (B), and spatial independency (C) of global model residuals for the GLMs evaluating the effects of fragmentation and habitat loss on generalist species abundance.

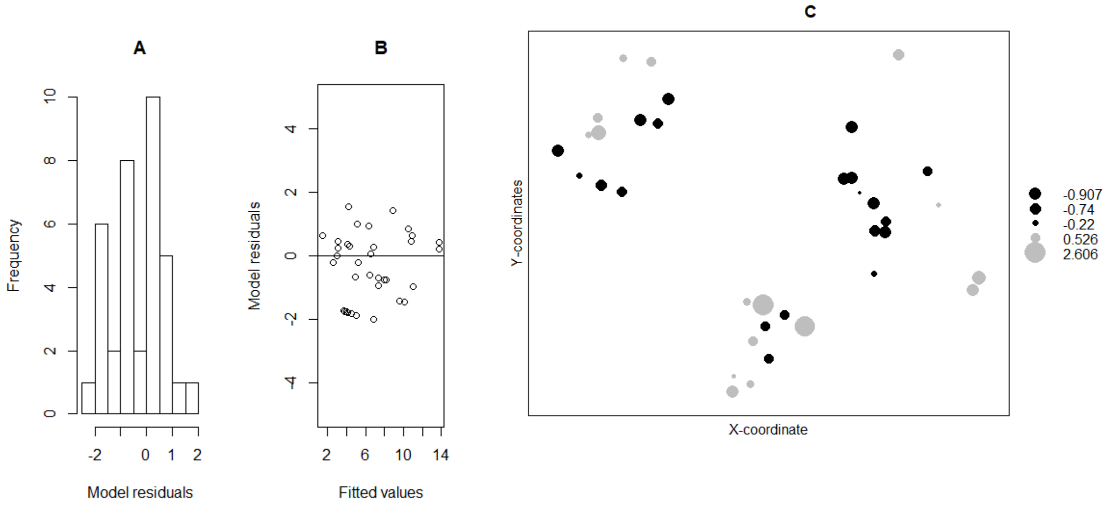

Figure AII. Model assumptions of normality (A), homogeneity (B), and spatial independency (C) of global model residuals for the GLM evaluating the effects of fragmentation and habitat loss on specialist species abundance.

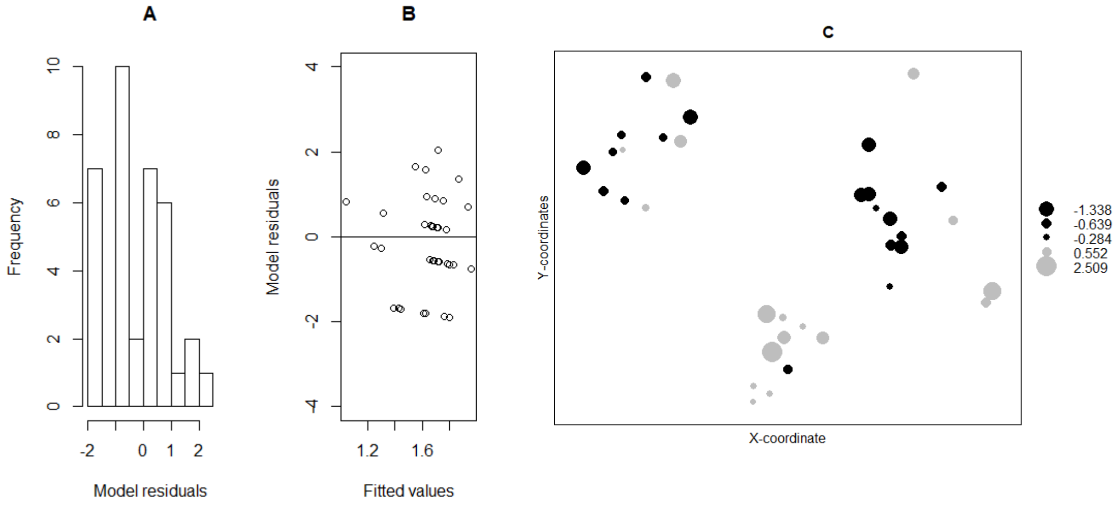

Figure AIII. Model assumptions of normality (A), homogeneity (B), and spatial independency (C) of global model residuals for the GLM evaluating the effects of fragmentation and habitat loss on estimated species richness of specialists.

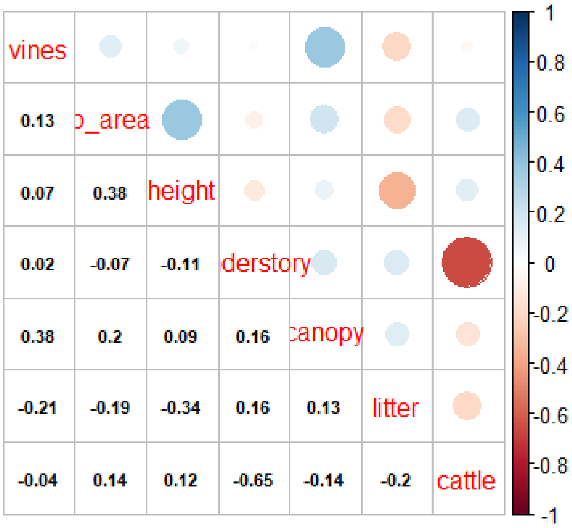

Figure AIV. Correlation plots (based on Pearson's correlation coefficients) investigating multicollinearity (r > 0.5) in the explanatory variable data set used as descriptors of habitat quality in PCA analyses: vines – number of vines; b_area – basal area (m²); height – tree height (m); understory – understory clutter (%); canopy – canopy cover (%); litter – litter volume (m³); cattle – level of cattle intrusion inside the patch;

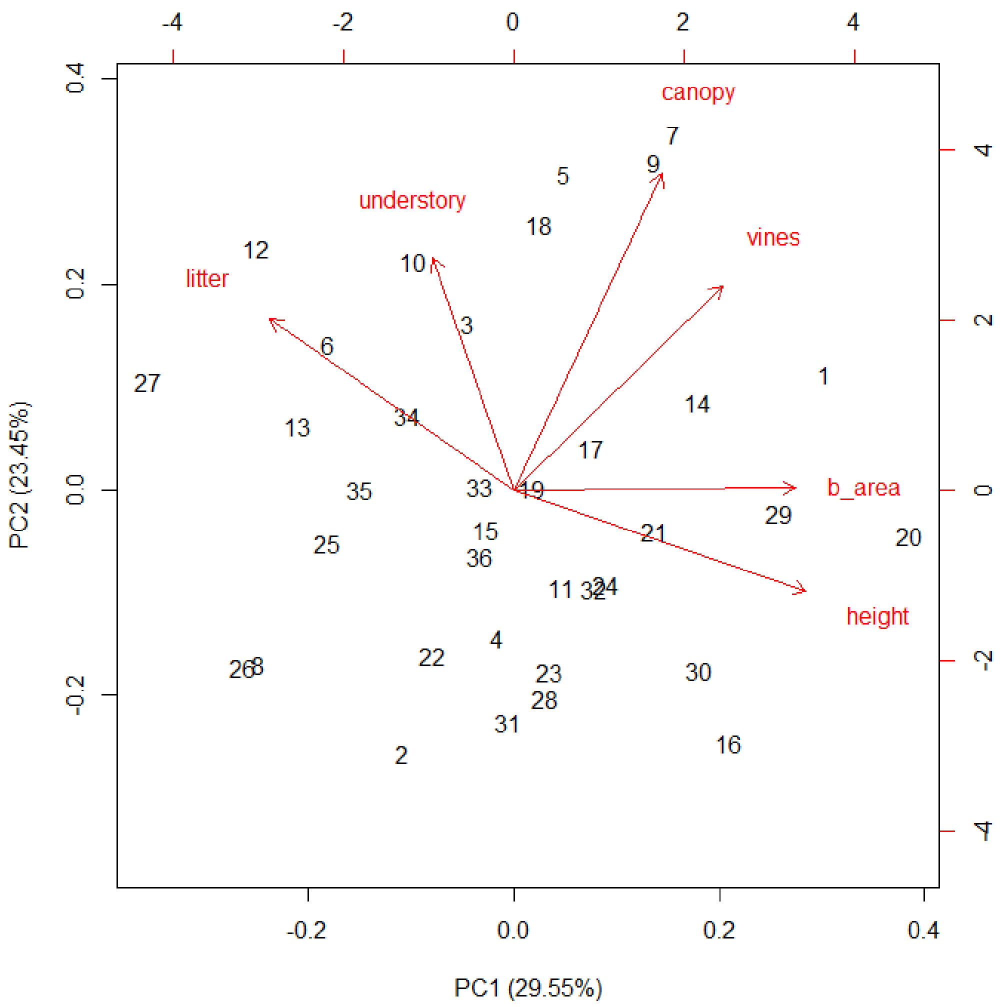

Figure AV. Principal component analysis of habitat structure variables describing habitat quality of semideciduous forest patches in the Brazilian Cerrado in central Goiás. vines – number of vines; b_area – basal area (m²); height – tree height (m); understory – understory clutter (%); canopy – canopy cover (%); litter – litter volume (m³);

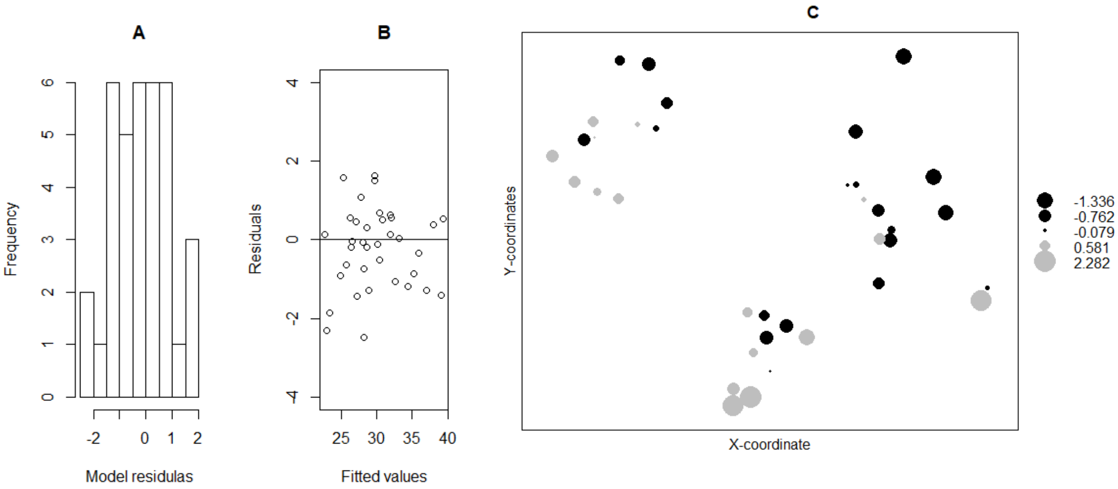

Figure AVI. Model assumptions of normality (A), homogeneity (B), and spatial independency (C) of global model residuals for the GLM evaluating the effects of habitat quality on abundance of generalist species.

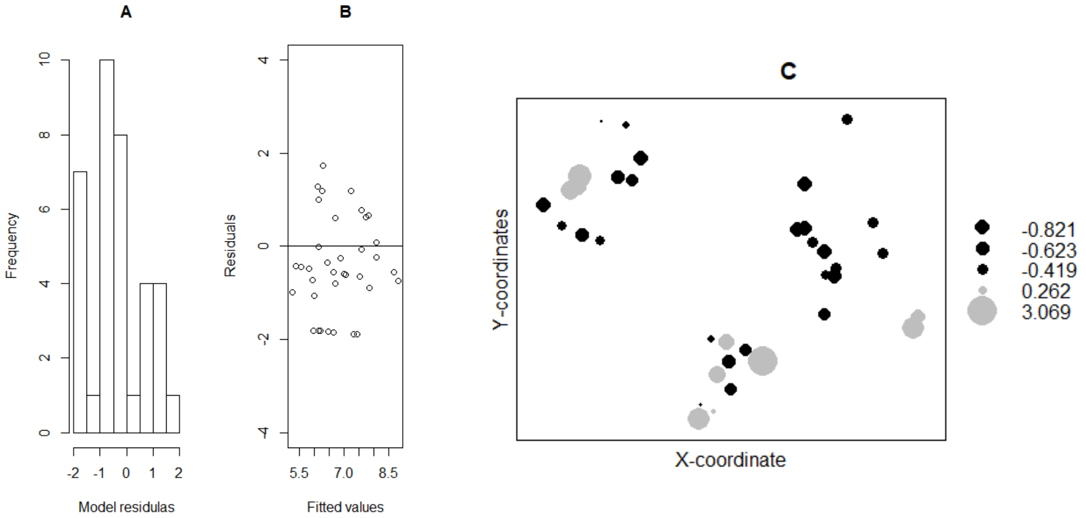

Figure AVII. Model assumptions of normality (A), homogeneity (B), and spatial independency (C) of global model residuals for the GLM evaluating the effects of habitat quality on abundance of specialist species.

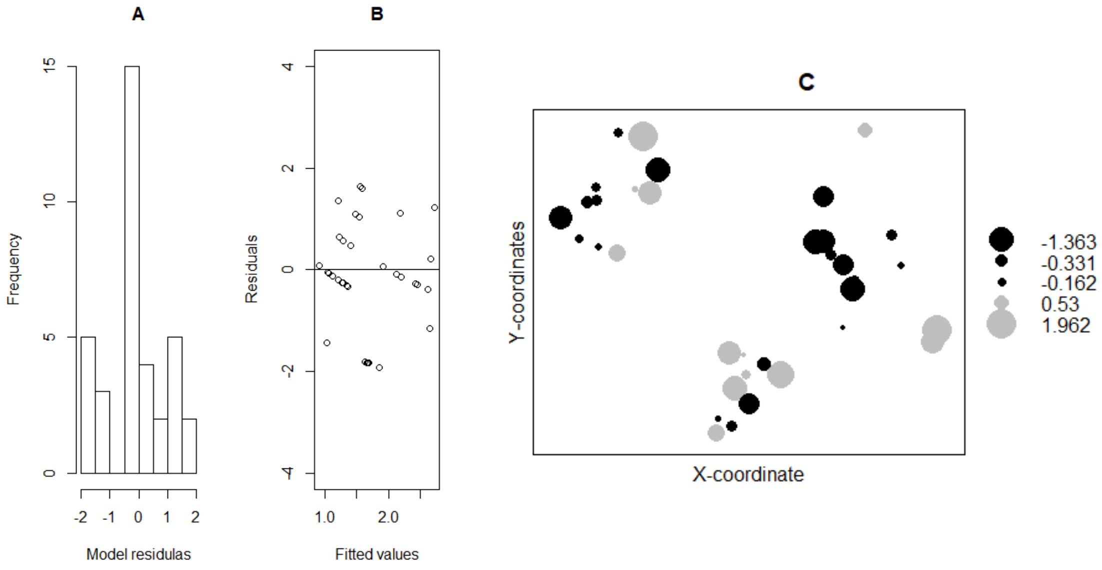

Figure AVIII. Model assumptions of normality (A), homogeneity (B), and spatial independency (C) of global model residuals for the GLM evaluating the effects of habitat quality on estimated richness of specialist species.

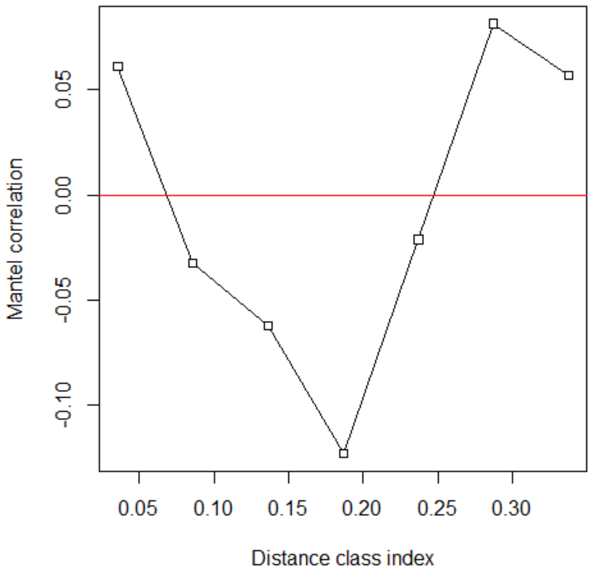

Figure AIV. Mantel correlogram generated for testing spatial autocorrelation between the species composition distance matrix with Hellinger transformation and the distance matrix of geographic coordinates of sampling sites. Significant correlations are indicated by black squared in the plot classes.

Table AI. Morphological and behavior traits used to estimate functional diversity.

Species	Habitat use[Ψ]	Diet[ψ]	Tail length	Hind feet width	Body weight (g)	Arboreality
Cryptonanus agricolai	Generalist	In/Om	1.48	0.58	19	0.83
Calomys expulsus	Generalist	Fr/Gr	0.83	0.29	26	0.08
Calomys tener	Generalist	Fr/Gr	0.86	0.24	15	0.00
Didelphis albiventris	Generalist	Fr/Om	1.04	0.54	558	0.04
Gracilinanus agilis	Generalist	In/Om	1.42	0.61	26	0.85
Hylaeamys megacephalus	Specialist	Fr/Gr	1.01	0.24	44	0.07
Marmosa demerarae	Specialist	In/Om	1.47	0.60	78	0.88
Marmosa murina	Specialist	In/Om	1.42	0.58	36	0.75
Oecomys catherinae	Specialist	Fr/Se	1.09	0.31	54	0.75
Oecomys cleberi	Specialist	Fr/Se	1.15	0.34	30	0.86
Oligoryzomys mattogrossae	Specialist	Fr/Gr	1.45	0.23	19	0.20
Oligoryzomys moojeni	Specialist	Fr/Gr	1.48	0.25	16	0.00
Oligoryzomys nigripes	Generalist	Fr/Gr	0.94	0.17	30	0.00
Rhipidomys macrurus	Specialist	Fr/Se	1.28	0.37	54	0.86
Rattus rattus	Generalist	Fr/Om	1.24	0.27	58	0.00

Following: [Ψ] Bonvicino et al. (2002); Marinho-Filho et al. (2002); Pardini (2004); Bezerra et al. (2009); Cáceres et al. (2010); Oliveira and Bonvicino (2011); Rossi et al. (2011); Gomes et al. (2015); Ribeiro (2015); [φ] Paglia et al. (2012); Shiels et al. (2014); Riofrío-Lazo and Páez-Rosas (2015).

Table AII. Autocorrelation test values based on Moran´s I, overdispersion test values based on Pearson residuals for residuals of all fitted GLM models (landscape structure analyses and habitat quality analyses) and significance of global models. Test results are expressed as p-values. Significant values are in bold.

Global regression model		Moran´s I test	Overdispersion test	Model significance
Landscape structure analyses:				
Y ~ log (patch area) * landscape				
Y	Generalists abundance	**0.04**	0.41	**3.01×10^{-4}**
	Specialists abundance	**1.6×10^{-3}**	0.65	0.07
	Estimated generalist species richness	0.81	0.99	0.22
	Estimated specialist species richness	**1.4×10^{-4}**	0.31	0.81
	Species diversity (Shannon)	0.65	0.83	0.58
	FD	0.78	1.00	0.68
Habitat quality analyses				
Y ~ PC1 + PC2				
Y	Generalists abundance	**0.02**	0.54	0.32
	Specialists abundance	**6×10^{-4}**	0.45	0.85
	Estimated generalist species richness	0.44	0.99	0.93
	Estimated specialist species richness	0.02	0.61	**0.05**
	Species diversity (Shannon)	0.49	0.86	0.43
	FD	0.99	1.00	0.49

Table AII. Significance of model predictors in model selection procedure of the analyses of the effects of habitat fragmentation and habitat loss in small mammal community metrics in semideciduous forest patches in the Brazilian Cerrado in central Goiás. The significance of a predictor was determined by likelihood ratio tests (LRT) or changes in Scaled deviance (depending on model error family) and by p-values generated by comparing nested models that drop variables in a stepwise approach. Significant values are in bold. Global model in all analyses: Y ~ landscape*log(patch area).

Response variable/ family distribution	**Predictors**	**df**	**Test**	**p**
			LRT	
Generalist abundance/ Negative binomial	landscape : log(patch area)	1	1.207	0.272
	landscape	1	5.493	**0.019**
	log(patch area)	1	19.470	**1.022 x 10^{-5}**
Specialist abundance/ Negative binomial	landscape : log(patch area)	1	0.036	0.849
	landscape	1	0.509	0.476
	log(patch area)	1	7.311	**0.007**
			Scaled deviance	
Estimated richness for generalists/Gamma	landscape : log(patch area)	1	0.002	0.965
	landscape	1	4.079	**0.043***
	log(patch area)	1	0.488	0.498
Estimated richness for specialists/ Poisson	landscape : log(patch area)	1	0.723	0.395
	landscape	1	0.025	0.873
	log(patch area)	1	0.208	0.648

Shannon diversity/ Gaussian	landscape : log(patch area)	1	0.461	0.497
	landscape	1	0.005	0.944
	log(patch area)	1	1.651	0.199
Functional diversity/ Gamma	landscape : log(patch area)	1	0.302	0.582
	landscape	1	1.116	0.291
	log(patch area)	1	0.122	0.726

Table AIII. Results of the Principal Component Analysis (PCA) obtained from six habitat variables to compare forest structure in 36 semideciduous forest patches in the Brazilian Cerrado. Values are the coefficient of the corresponding eigenvectors. More heavily loaded variables are in bold (loading ≥ 0.5).

Variables	**PC1**	**PC2**
Vines	0.38	0.42
B_area	**0.52**	0.00
Mean tree height	**0.54**	-0.21
Understory clutter	-0.15	0.48
Canopy cover	0.27	**0.65**
Litter volume	-0.45	0.35
Variance explained (%)	29.55	23.45

Table AIV. Significance of model predictors in model selection procedure of the analyses on the effects of habitat quality in small mammal community metrics in semideciduous forest patches in the Brazilian Cerrado in central Goiás. The significance of a predictor was determined by likelihood ratio tests (LRT) or changes in deviance (depending on model error family) and by p-values generated by comparing nested models that drop variables in a stepwise approach. Significant values are in bold. Global model in all analyses: Y ~ PC1 + PC2.

Response variable/ family distribution	**Predictors**	**df**	**Test**	**p**
			LRT	
Generalist abundance/ Negative binomial	PC1	1	0.993	0.318
	PC2	1	0.252	0.615
Specialist abundance/ Negative binomial	PC1	1	0.135	0.713
	PC2	1	0.192	0.661
			Scaled deviance	
Estimated richness for generalists/Gamma	PC1	1	0.091	0.762
	PC2	1	0.048	0.825
Estimated richness for specialists/ Poisson	PC1	1	0.300	0.583
	PC2	1	5.536	**0.018**
Shannon diversity/ Gaussian	PC1	1	1.464	0.226
	PC2	1	0.327	0.566
Functional diversity/ Gamma	PC1	1	0.888	0.345
	PC2	1	0.517	0.472

Capítulo 2

Changes in the isotopic niche space of a didelphid opossum in fragmented landscapes with distinct levels of habitat loss in a neotropical savanna

Authors: Mattos, I; Ribeiro, J.F.; Nardoto, G.B.; Zimbres, B.; Marinho-Filho, J.

Abstract

Habitat loss and fragmentation can affect species trophic ecology. However, the impacts of fragmentation may depend on the remaining habitat amount in the landscape, and are expected to be stronger at intermediate levels of habitat availability, where configuration might have the greatest variability. We used stable carbon and nitrogen isotopes to investigate how fragmentation alters isotopic niche space of the marsupial *Gracilinanus agilis* depending on levels of habitat loss in semideciduous forests in the Brazilian savanna. We predicted that the opossum should present a higher input of matrix resources (increased δ^{13}C values) in smaller patches, and this would be stronger in the more degraded landscape. Also, we expected a niche shift from small to large patches with an increase in δ^{15}N values. Moreover, we expected either a niche collapse or a niche expansion with fragmentation, and these effects would be stronger in intermediate landscapes. Contrary to our expectations, δ^{13}C did not vary with patch size nor habitat loss, with values revealing a high dependency on forest resources. The opossum presented a niche shift only in intermediate and more conserved landscapes, transiting from insectivory to frugivory from small to large patches, respectively. This effect was stronger in the former landscape, probably due to higher fruit availability in larger patches in more conserved landscapes. Finally, we found a niche expansion towards smaller patches in the most degraded landscape, likely because of the addition of less valuable dietary items under a context of low food availability and high forager density. Conversely, there was a niche expansion towards larger patches (in other words, a niche collapse following fragmentation) that was progressively marked from intermediate to more conserved landscapes, probably owed to higher resource availability/diversity associated with habitat quality and forest complexity. We recorded changes in the opossum´s trophic ecology within the fragmentation gradient depending on landscape context of habitat loss and showed that these human driven alterations modifies niche breadth, trophic structure and its ecological role (e.g., shifts in trophic level), hampering the species potential as a seed disperser in small remnants. Despite these consequences, we argue that even small patches are important to maintain opossum´s population in hyper fragmented landscapes, since it is highly dependent on forest resources.

Keywords: Cerrado, feeding habits, *Gracilinanus agilis*, habitat amount, stable isotopes

Introduction

Landscape alterations are the main drivers of global biodiversity decline, also affecting trophic relations (Estes et al. 2011; Haddad et al. 2015). In the tropics, habitat changes result mostly from forest conversion to agriculture and pasture (Gibbs et al. 2010; Françoso et al. 2015; Strassburg et al. 2017). Although habitat loss has large negative impacts to ecosystems, fragmentation per se (i.e., controlling for habitat amount in the landscape) can both benefit generalist and tolerant species and jeopardize specialist ones (Fahrig 2019; Pardini et al. 2010; Hanski 2015; Melo et al. 2017). However, impacts of fragmentation (i.e., habitat configuration) may depend on the remaining habitat amount in the landscape, and are expected to be stronger at intermediate levels of habitat availability, influencing animal movement across the landscape and consequently species persistence (Martensen et al. 2012; Pardini et al. 2010; Villard & Metzger 2014). Also, the relative tolerance to changes in habitat configuration may restrict or expand the range of habitat amount over which a species can occur (Villard and Metzger 2014).

These responses may depend on species ecological traits (Purvis et al. 2000; Davies et al. 2004; Haddad et al. 2015) related to matrix tolerance, dispersal ability, diet, and trophic level (Davies et al. 2000; Boyle & Smith 2010; Newbold et al. 2012; Keinath et al. 2017; Magioli et al. 2019). Therefore, the consequences of habitat loss and fragmentation might be reflected in changes in a species trophic niche (Layman et al. 2007b; Resasco et al. 2018; Muñoz-Lazo et al. 2019). The ability to persist in human-modified landscapes should depend on species trophic plasticity, i.e., whether it can survive on the resources available within patches, shifting to new food resources or/and including food items previously not exploited (Resasco et al. 2018; Muñoz-Lazo et al. 2019), and potentially incorporating matrix resources (Magioli et al. 2019). In this sense, it is urgent to understand not only the ecology of most susceptible species to the effects of landscape conversion, but also of resilient species that are capable to persist in altered habitats (Layman et al. 2007b) as species loss advances, and deforestation rates still grow (Ceballos et al. 2015; Nowosad and Stepinski 2019).

Research on diet, trophic niche, and habitat use have been increasingly studied under the perspective of stable isotope analyses of carbon (^{13}C) and nitrogen (^{15}N) (see Layman et al. 2012; Magioli et al. 2019; Ribeiro et al. 2019). Isotopic carbon ratios ($\delta^{13}C$)

provide tracks on habitat use of foraging areas, since this ratio varies substantially amongst primary producers with different photosynthetic pathways (e.g., C_3 trees and shrubs in forests; and C_4 grasses in savannas and grasslands), but hardly changes through trophic levels (Ben-David and Flaherty 2012). Isotopic nitrogen ratios (δ^{15}N) reveal trophic position, because there is an enrichment of ^{15}N to ^{14}N at each trophic level in a food web or community (Post 2002; Ben-David and Flaherty 2012). Therefore, stable isotopes have great potential to contribute to the understanding of the impacts of habitat conversion, fragmentation, and habitat loss on species trophic ecology, also revealing how animals shift their resource use among continuous forests, isolated habitat patches, and the matrix (Layman et al. 2012; Resasco et al. 2018; Magioli et al. 2019; Muñoz-Lazo et al. 2019).

In this study, we investigated how fragmentation (i.e., habitat configuration) may alter isotopic trophic ecology of the omnivorous-insectivorous didelphid agile opossum *Gracilinanus agilis* (Burmeister, 1854) depending on landscape context of habitat loss in a fragmentation gradient in semideciduous forests in the Brazilian savanna. Non-flying small mammals (Rodentia and Didelphimorphia) are potential indicators of environmental quality (Bonvicino et al. 2002), and are an ideal group to assess human-driven landscape modifications in trophic ecology. They are abundant, perform key roles in ecosystems and respond to resource availability, environmental, and landscape changes (Brown et al. 2001; Previtali et al. 2009; Pardini et al. 2010; Kajin and Grelle 2012). We asked the following questions: (i) do the increase of fragmentation (represented by patch size) and habitat loss (represented by total habitat amount in the landscape) lead the agile opossum to incorporate matrix resources (i.e., an increase in δ^{13}C values)? (ii) does fragmentation (i.e., patch size) cause a shift in trophic position of the marsupial depending on landscape context of habitat loss (i.e. an increment in δ^{15}N values)? (iii) does isotopic niche space (i.e., trophic diversity) change with patch size depending on the remaining habitat amount in the landscape? We expected an input in the assimilation of matrix resources in smaller patches (higher δ^{13}C values), specially within the more degraded landscape (Magioli et al. 2019; Ribeiro et al. 2019), if the opossum is able to forage in the matrix or matrix arthropods can enter patch edges (Pompermaier et al. 2020). Also, we predicted an overall increase in the trophic position of *G. agilis* towards smaller patches, and we expected this relation to be stronger in the intermediate landscape followed by the more conserved landscape. Since fragmentation and habitat loss alters forest dynamics and results in a reduction of fruit availability (Terborgh 1992), we hypothesized the agile opossum would consume more insects in smaller fragments and more fruits in larger ones. Finally, we predicted two responses in isotopic niche space (i.e., niche diversity) with fragmentation, that should be more intense within intermediate levels of habitat amount.: (i) niche collapse, if the opossum tracks the lower abundance/diversity of food resources expected by the species-area relation (Lomolino 2001; Layman et al. 2007b), and by low fruit availability in smaller patches (Terborgh 1986, 1992); or (ii) a niche expansion, as an outcome of trophic plasticity, allowing the agile opossum to include in its diet least valuable food items - especially if it is able to forage on matrix resources (Magioli et al. 2019; Ribeiro et al. 2019).

Furthermore, since habitat amount is related to landscape connectivity (Fahrig 2003, 2013), a severely disrupted landscape presents fewer opportunities for foraging among different patches, thus reducing diversity of potentially ingested food items, which contributes to an overall tendency of reduction or expansion of niche space across patches of varying sizes. Thus, in this landscape we expected the effect of patch size to be weak. Accordingly, in the more conserved landscape, where connectivity is high, it is expected that the consumer forages across different patches, leading to a similarity in niche space in patches of different sizes. Consequently, we also predicted a soft effect of patch size (positive or negative) in niche space in this condition of habitat availability. Finally, we expected to find the strongest effect of patch size in niche space (either positive or negative) within the intermediate landscape, where connectivity is moderate, driving patch size to become more important to determine the foraging behavior of the agile opossum.

Materials and methods

Study area

The study was conducted in remnants of semideciduous seasonal forests in three landscapes of ~15,000 ha with different levels of habitat amount (~ 10, 25, and 40 %) in a highly deforested portion in the Brazilian Cerrado. In each landscape we sampled 12 forest patches (totaling 36 sampling sites), ranging from 2 to 760 ha, where small mammals were surveyed. Sampling patches were located in the municipalities of Abadiânia (16º2´51´´ S 48º51´44´´ W), Jesúpolis (15°57´05´´ S 49°22´26´´ W), Jaraguá (15º44´31´´ S 49º20´6´´ W), Ouro Verde de Goiás (16°13´13´´ S 49°11´36´´ W), Pirenópolis (15°53´06.40´´ S 49°10´46.29´´ W), and São Francisco de Goiás (15º55´51´´ S 49º15´2´´ W), in the central portion of the state of Goiás, Brazil. In these regions, the matrix is comprised mainly of pasture, but there are also agricultural areas (such as crop fields and/or banana plantations) and few natural patches of savanna vegetation. Sampling sites were located in the Legal Reserves of private farms, which are the natural vegetation area all landowners are legally obliged to preserve. The climate is classified as Aw according to Köppen, with two well defined climatic seasons (hot/wet summers from October to March, and dry/cold winters from April to September).

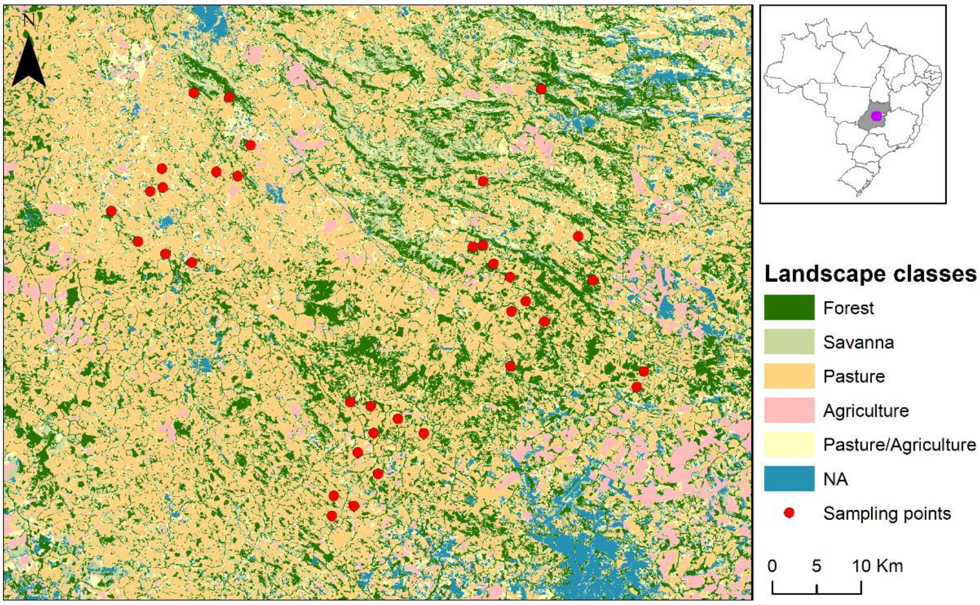

Figure 1. Landscapes of 15.000 ha with 10, 25 e 40% of habitat amount (including both forest and savanna), and the sampled patches (red dots) in central Goiás state, Brazil (highlighted in grey in the inset map). Patches located in the western portion of the map represent the landscape with 10% of remnant habitat amount, those located in the middle correspond to landscape with 25%, and the eastern patches are in the landscape with 40% of habitat amount.

Studied species

The agile opossum *Gracilinanus agilis* (Burmeister, 1854) is a small bodied (20-30 g), solitary, nocturnal, didelphid marsupial with arboreal and scansorial habits (Emmons and Feer 1997). It feeds mostly on arthropods (mainly Hymenoptera, Isoptera, Hemiptera, and Coleoptera), small fruits, and occasionally birds (Camargo et al. 2014). Also, it presents a seasonal variation in its diet, with reproductive females feeding more heavily on insects during the mating season (Camargo et al. 2014). Additionally, a study on the isotopic diet of this species corroborated a high arthropod consumption, and revealed that forest-resident individuals can switch between prey resources from forests (C_3) in the rainy season to those from grasslands (C_4) in the dry season (Ribeiro et al. 2019). Reproduction occurs seasonally, from the end of the cool-dry season to mid/end of the warm-wet season (Lopes and Leiner 2015). This marsupial has a wide geographic distribution in South America, ranging over the east of the Andes in Peru, Bolivia, Paraguay, Uruguay, and Argentina (Emmons and Feer 1997). In Brazil, it inhabits the Cerrado, Caatinga, and

Pantanal biomes (Paglia et al. 2012), where it is commonly found in forest formations, e.g. gallery forests, dry forests, and woodland savannas (Vieira and Palma 2005).

Small mammal capturing

In each of the 36 sampled patches, we established a trap line of 200 m, located 30 m from the patch edges to avoid edge effects. Each line had 20 trap stations, placed every 10 m, with four livetraps each, where half were set on the ground, and half in the understory (at least 1.5 m height). Every station had a Tomahawk®(300 x 160 x 160 mm) and a small Sherman® (250 x 80 x 90 mm) on the ground, and a big Sherman (300 x 80 x 90 mm) and a small one in the understory, except for the first and last trap stations, where we replaced a Tomahawk trap by a big Sherman. The study was conducted over the year 2018 between the rainy-dry season (April-June) and the dry-rainy one (August-October), thus considering seasonal variations in diet. Captures occurred for four consecutive nights per field campaign, resulting in an effort of 640 trap-nights per patch and 23,040 trap-nights in total.

Traps were baited with a mixture of peanut butter, corn powder, sardine, and banana. Captured animals were identified, marked with numbered ear-tags, measured and weighted. We also recorded age (following Macedo et al. 2006), gender, and reproductive status. We collected a hair sample from the posterior dorsal region from all individuals with a clean scissor, and stored samples in plastic tubes. Animals were released in the same trap location where they were captured. Voucher specimens were collected and held in the Mammal Collection of the Department of Zoology, University of Brasília (UnB, Brasília, Brazil). All procedures followed the guidelines of the American Society of Mammalogists for the use of wild animals in research (Sikes *et al*. 2016). We conducted the study under the permission of the Committee of Ethics and Animal Use from the University of Brasília (28/2018), Instituto Chico Mendes de Biodiversidade (SISBIO 61990) and Secretaria de Meio Ambiente do Estado de Goiás (SECIMA/CEMan 006/2019).

Landscape structure

We chose landscapes based on the 2016 land use and land cover map from the MapBiomas project, collection 4.0, which classifies Landsat 8 satellite imagery at a 30-m resolution. The temporal mismatch between the land cover map from MapBiomas and the field campaigns should be important, since the study sites are within a relatively consolidated landscape in terms of human occupation. Landscape choice was based on the proportion of five land use classes: forest, savanna, agriculture, pasture, and mosaic of agriculture and pasture [see MapBiomas class description in (http://mapbiomas.org)].

Landscape structure was evaluated as patch size (ha) and proportion of habitat amount available in each landscape context [10, 25 and 40% of natural cover (forest plus savanna) as shown in Fig. 1]. These metrics were calculated using the Patch Analyst extension in ArcGis 10.2. We grouped patches into classes of size on a log scale (Norris et al. 2010) to represent a gradient of fragmentation, indicated in Table 1. From this point on, we will refer to patch size classes 1, 2, and 3 to indicate the gradient of size representing small (class 1), medium (class 2), and large (class 3) patches.

Isotopic analysis

We collected hair samples of at least three individuals of *Gracilinanus agilis* per patch, whenever possible (but we did not discard patches where we could only get one or two samples). In addition, to avoid bias in isotopic values we excluded samples from four patches that were surrounded by soy or banana plantations, since our focus was on the most prevalent pasture matrix. Thus, we analyzed 98 samples from individuals captured in 30 of the 36 sampled patch sites (there were two patches where we did not capture any *G. agilis* individuals). Also, we tried to equally distribute samples among sexes and excluded juveniles to avoid possible bias in isotopic values towards gender and age differences in trophic niche. Hair samples were washed with distilled water, subsequently immersed in a 2:1 solution of chloroform and methanol for 30 min, and washed again with distilled water. Afterwards, samples were oven dried for 12 hours at 65º, shredded and weighted (minimum aliquot of 1.5 mg) in tin capsules on an analytical scale (0.001 g precision) (Ribeiro et al. 2019).

Isotopic analyses were performed at the Stable Isotope Facility of the University of California (SIF), Davis, USA. Samples were analyzed for ^{13}C and ^{15}N isotopes using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). During analysis, samples were interspersed with several replicates of at least four different laboratory reference materials. These reference materials have been previously calibrated against international reference materials, including: IAEA-600, USGS-40, USGS-41, USGS-42, USGS-43, USGS-61, USGS-64, and USGS-65 reference materials. A sample's provisional isotope ratio is measured relative to a reference gas peak analyzed with each sample. These provisional values are finalized by correcting the values for the entire batch based on the known values of the included laboratory reference materials. The long term standard deviation is 0.2 per mil for ^{13}C and 0.3 per mil for ^{15}N.

The results were expressed in delta notation (δ), in parts per thousand (‰), based on internationally recognized standards. We used the following equation: δ^{15}N or δ^{13}C (‰) = $(R_{sample} - R_{standard}) / R_{standard} \times 1.000)$, where R_{sample} and $R_{standard}$ represent the heavy/light isotope molar ratio of the sample and standard, respectively. The standard used for carbon analysis was Vienna Pee Dee Belemite (Vienna PDB; ^{13}C:^{12}C ratio = 0.01118), and the standard used for nitrogen analysis was atmospheric air (^{15}N:^{14}N ratio = 0.0036765).

Table 1. Number of studied patches of semideciduous forests in the Brazilian Cerrado from each size class over the landscape gradient of habitat amount (10, 25, 40% of natural cover), and total number of *Gracilinanus agilis* hair samples per patch size class used in isotopic analysis.

				Nº patches			Nº of isotopic samples		
				Landscape gradient of habitat amount (%)					
Size class	Interval (ha)	Mean ± SD	Range/min-max (ha)	10	25	40	10	25	40
C1	0 - 10	5.52 ± 2.29	2 - 10	3	2	3	9	6	10
C2	11 - 100	46.39 ± 26.84	13 - 91	5	3	4	22	9	10
C3	101 -1000	236.56 ± 207.44	121 - 760	4	3	3	16	10	6
Mean				4	3	3	16	8	9
Total				12	8	10	47	25	26

Data analysis

Habitat use and trophic position

To evaluate whether fragmentation and habitat loss leads the agile opossum to incorporate matrix resources (which means an increase in δ^{13}C), and to test if fragmentation causes a shift in trophic position (i.e., changes in δ^{15}N values) depending on landscape context of habitat amount, we compared nested linear mixed models (LMM) with likelihood ratio test (LRT). We used LMM since residuals were normally distributed (Fig. 1A - Appendix I), and to account for differences in the number of isotopic samples between patch sites, including *site* as a random effect; the following variables – and the interaction between them – were included as fixed effects: 1) *Patch size class*, a categorical variable representing fragmentation (following Table 1), with three levels (small, class 1: C_1; medium, class 2: C_2; large, class 3: C_3) ; 2) *Habitat amount in the landscape* (%), a categorical variable representing the gradient of habitat loss in the landscape, with three levels (landscape 10%, landscape 25%, landscape 40%). The significance of explanatory variables was given by changes in Deviance and p-values resulting of LRTs between all combinations of nested models built by dropping variables in a stepwise approach. We fit models using the *lme4* package (Bates et al. 2015), and performed model validation following Zuur et al. (2009) (Fig. 1A, Table 1A - Appendix I) in R, version 3.6.2 (R Core Team 2019).

Isotopic niche space

Isotopic niche metrics are based on mean values of δ^{13}C – δ^{15}N from *G. agilis* individuals dispersed in isotopic niche space, represented by a biplot. These metrics reveal important aspects of trophic structure and are related to trophic diversity (Layman et al. 2007a; Jackson et al. 2011). Therefore, to evaluate possible shifts in *G. agilis* trophic niche along the gradients of fragmentation and habitat loss, we calculated the standard ellipse areas corrected for small sample size (SEAc), a bivariate standard deviation that represents the core isotopic niche space of a population (Jackson et al. 2011). For this, we pooled isotopic samples according to patch size classes (Table 1) nested within each landscape (10, 25, and 40%). Thus, we were able to compare the effects of patch size per se depending on landscape context of habitat loss. Also, we ensured we had at least five samples per size class/landscape to estimate SEAc (Jackson et al. 2011). We compared size, position and niche overlap between ellipses from patch size classes within landscapes. These analyses were conducted in R software version 3.6.2 (R Core Team 2019) using the *SIBER* package (Jackson et al. 2011).

Results

Habitat use and trophic position

We analyzed 98 hair samples of *G. agilis* captured in 30 patches ranging from 2 to 760 (ha). Sample size per patch size classes within landscapes ranged from 6 to 22 samples, and are shown in Table 1. Mean values of $\delta^{13}C$ were similar across patch size classes within landscapes, ranging from -25.91 to -22.84‰ (Table 2, Fig.2, Fig. 2A – Appendix I). This interval of $\delta^{13}C$ values revealed that individuals assimilated mostly forest patch resources (C_3) and practically no resources from the pasture matrix (C_4), regardless of patch size and habitat loss context, contradicting our hypothesis (Table 2, Fig. 2, Fig.2A – Appendix I). Patch size class and habitat amount in the landscape had no effect on $\delta^{13}C$ values (Table 3, Patch size class, p = 0.6584; Landscape, p = 0.3505; Table 1A – Appendix I).

The agile opossum presented a great variation in $\delta^{15}N$ values, ranging from 3.87 to 9.69‰ (Fig.2, Fig. 3A – Appendix I). These values indicate it is an omnivore-insectivore with great trophic plasticity, presenting a diet that comprises frugivory up to third level predation (Table 2). The model that best explained variation in $\delta^{15}N$ values included a significant interaction of patch size class with habitat amount in the landscape (Deviance = 242.8, χ^2 = 22.503, df = 4, p = 0.0001), which means the effects of fragmentation on $\delta^{15}N$ values depended on landscape context (Table 1A, 2A – Appendix, Fig. 2). In the most degraded landscape (10%), $\delta^{15}N$ values were similar irrespective of patch size, ranging from 6.09‰ in average in small patches towards an increase of 0.88‰ and 0.30‰ in medium and large patches, respectively (Table 2, Table 3, Table 2A – Appendix, Fig. 2). These values indicate the agile opossum occupies approximately the same trophic level and feeds on similar food items (likely invertebrates) regardless of fragmentation level. Moreover, in this extreme context of habitat loss, we found a similarly high range of $\delta^{15}N$ values across all patch size classes (C1, 4.29 to 8.07‰; C2, 4.84 to 8.07‰; C3, 4.27 to 8.89‰), indicating an even generalist feeding habit and a wide trophic niche width at the population level in this landscape. However, we found a negative relation of $\delta^{15}N$ values with patch size in landscapes with intermediate (25%) and high (40%) levels of remnant habitat amount. According to our hypothesis, this effect was stronger in the intermediate landscape (25%), with an estimated reduction of 2.75‰ in $\delta^{15}N$ values from small (C1, 8.34‰) to large patches (C3, 5.59‰), corresponding to shifts of almost two trophic levels (Table 2, Table 3, Table 2A – Appendix, Fig. 2). The most conserved landscape (40%) showed a slightly declining pattern of $\delta^{15}N$ values from small to large patches with an estimated reduction of 1.62‰. Also, $\delta^{15}N$ values reached much lower levels in larger patches (C1, 6.47‰; C3, 4.85‰), indicating a more consistent contribution of basal resources (fruits and C_3 leaves) when there is more habitat available at the landscape level (Table 2, Table 3, Table 2A – Appendix, Fig. 2).

Table 2. Isotopic mean values of δ^{13}C, δ^{15}N, and standard deviation (mean ± SD) of *Gracilinanus agilis* hair samples in patch size classes within the landscape gradient of habitat amount (10, 25, 40% of natural cover) in semideciduous forests in the Brazilian Cerrado.

Patch size class	Landscape					
	10 (%)		25 (%)		40 (%)	
	δ^{13}C (‰)	δ^{15}N (‰)	δ^{13}C (‰)	δ^{15}N (‰)	δ^{13}C (‰)	δ^{15}N (‰)
1	24.234 ± 0.768	6.093 ± 1.214	23.995 ± 0.443	8.348 ± 0.908	23.877 ± 0.749	6.487 ± 0.365
2	23.969 ± 0.865	6.965 ± 0.856	23.833 ± 0.700	6.512 ± 0.782	23.800 ± 0.681	6.039 ± 0.828
3	24.016 ± 0.705	6.386 ± 1.031	24.266 ± 0.802	5.523 ± 0.726	23.632 ± 0.719	4.843 ± 0.914

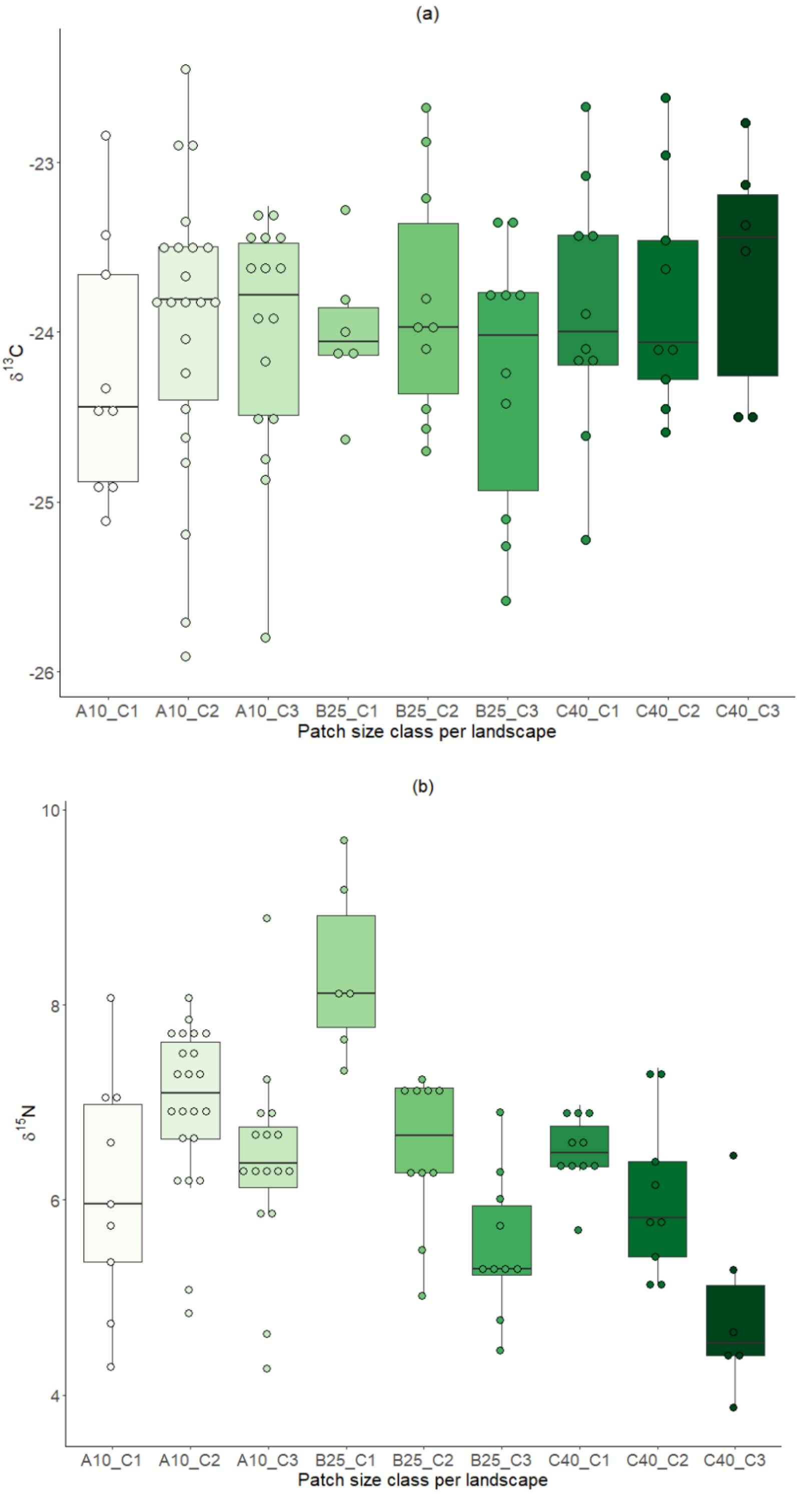

Figure 2. Distribution of δ^{13}C (a) and δ^{15}N (b) values of hair samples from *Gracilinanus agilis* across patch size classes within the landscape gradient of habitat amount (10, 25, and 40% of natural cover) in semideciduous forests in the Brazilian Cerrado. Landscapes with different remnant habitat amount are represented as follows: A10 – landscape with 10%; B25 – landscape 25%; C40 – landscape 40%; Patch size classes: C1 – class 1 (small); C2 – class 2 (medium); C3 – class 3 (large).

Table 3. Summary of the linear mixed model analyses of the effects of habitat fragmentation and habitat loss on agile opossum *Gracilinanus agilis* values of δ^{13}C and δ^{15}N hair contents. The significance of a variable was determined by changes in deviance and p-values generated by comparing nested models that drop variables in a stepwise approach. Significant values are indicated in bold.

δ^{13}C	**Variables**	**df**	**Deviance**	**χ^2**	**p-value**
	Patch size class: Landscape	4	212.890	4.879	0.770
	Patch size class + Landscape	2	214.840	1.947	0.746
	Patch size class	2	215.670	0.836	0.658
	Landscape	2	217.770	2.097	0.351
δ^{15}N	Patch size class: Landscape	4	242.800	37.295	**1.016×10^{-5}**
	Patch size class + Landscape	2	265.300	22.503	**1.591×10^{-4}**
	Patch size class	2	275.420	10.111	**0.006**
	Landscape	2	272.690	7.385	**0.025**

Isotopic niche space

Isotopic niche ellipses varied among patch size classes along the landscape gradient of habitat amount (Fig. 3), and overall shifts were linked to variation in δ^{15}N values. In the most eroded landscape (10%), isotopic niche ellipses were similar and overlapped more than 50% among patch size classes (Table 4). However, isotopic niche area (SEAc) from small patches (C1, 2.569‰^{2}) were 1.4 times larger than in large patches (C3, 1.815‰^{2}) (Fig. 3, Table 4). In intermediate and more conserved landscapes, we found a progressive niche shift downward in the biplot niche space from small to large patch size classes, indicating a higher contribution of basal resources with the increase of patch size and habitat amount in the landscape (Fig. 3). In these landscape contexts, ellipses between patch size classes were slightly overlapped (less than 50%, Table 4), and we found a progressive expansion of niche area from small to large patches in both landscapes, that was more prominent in the most conserved landscape (Landscape 25%: SEAc $_{C3}$ was 1.29 times larger than SEAc $_{C1}$; Landscape 40%: SEAc $_{C3}$ was 2.55 times larger than SEAc $_{C1}$, Fig. 3, Table 4).

In other words, under the lower fragmentation threshold (landscape with 10% or less of habitat amount), despite the similarity of niche position irrespective of patch size, there was a slight expansion of niche area with the reduction of patch size. With the increase of habitat amount in the landscape (landscapes with 25 and 40% of habitat amount), there was a progressive expansion of ellipse area (indicating higher trophic diversity) towards larger patches concurrently with the shift of trophic position from an omnivore–insectivore to a more basal resource diet.

Table 4. Standard ellipse area corrected for small samples (SEAc, ‰^{2}) and isotopic niche overlap (%) between ellipses for the agile opossum (*Gracilinanus agilis*) from patch size classes within the landscape gradient of habitat amount in semideciduous forests in the Brazilian Cerrado. Patch size classes: C1 – class 1; C2 – class 2; C3 – class 3.

	Habitat amount in the landscape		
	10%	**25 %**	**40 %**
Ellipses	**SEAc (‰^{2})**		
C1	2.569	1.575	0.964
C2	2.334	1.680	1.872
C3	1.815	2.041	2.461
Patch size class	**Isotopic niche overlap (%)**		
C1 - C2	57.8	29.2	42.6
C1 - C3	70.7	11.1	24.1
C2 - C3	57.5	42.5	45.9

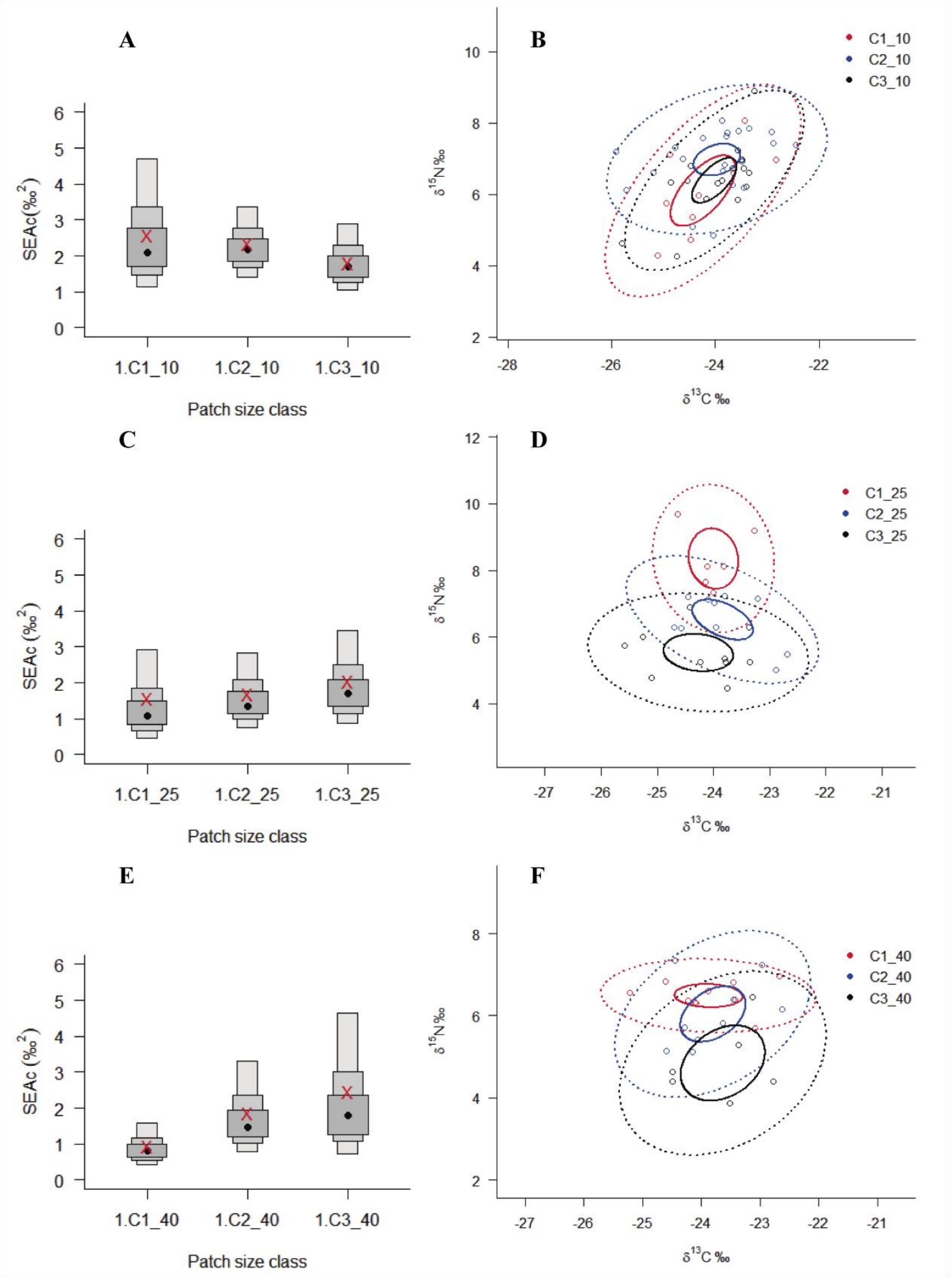

Figure 3. Standard ellipse area density plots and isotopic niche ellipses of hair samples from the agile opossum (*Gracilinanus agilis*) across patch size classes along the landscape gradient of habitat amount in semideciduous forests in the Brazilian Cerrado. Landscapes with different remaining habitat amount:10% (A, B); 25% (C, D); 40% (E,

F). In A, C, E, the red “X” represents standard ellipse area corrected for small samples (SEAc). Colors represent patch size classes: red – class 1 (C1); blue – class 2 (C2); black – class 3 (C3). Thick lines represent mean values and dotted lines, total values.

Discussion

Fragmentation effects on isotopic niche space of the agile opossum were dependent on the context of habitat loss, and were mainly linked to shifts in hair δ^{15}N. We did not detect changes in δ^{13}C values associated with fragmentation and/or habitat loss. However, δ^{13}C values indicated the species is highly dependent on forest resources (mostly C_3 found in hair samples). The agile opossum showed a small expansion in niche area towards smaller patches in the most degraded landscape, but there was no significant change in trophic position. At intermediate levels of habitat amount, there was a strong niche shift associated with a slight expansion of niche area from small to large patches. Finally, under a more conserved condition of habitat amount, we found a similar pattern as the latter described; however, niche shift was about one trophic level from small to large patches, and changes were towards much lower trophic position combined with a pronounced niche expansion. We suggest that there might be different ecological mechanisms underlying such changes, and they could present variable relative importance depending on landscape context (habitat amount), leading to distinct responses in the isotopic niche space.

Contrary to our predictions, we did not find effects of fragmentation and/or habitat loss in δ^{13}C values, revealing that *G. agilis* feeds on similar basal resources (mainly C_3) in all study patches, and it is highly dependent on forest remnants, which potentially indicates a low tolerance to pasture matrix under a trophic perspective (Magioli et al. 2019). Omnivorous mammal species can be able to incorporate C_4 resources from an agricultural matrix, leading to significant changes in δ^{13}C values between conserved and highly modified landscapes, while insectivorous species show no changes in δ^{13}C values, in accordance with *G. agilis* in our study (Magioli et al. 2019). Thus, the impacts of landscape conversion in a species’ feeding habits and habitat use, and its consequent ability to survive in fragmented environments might be linked to the species’s functional traits related to trophic guild (Layman et al. 2007b; Resasco et al. 2018; Magioli et al. 2019; Muñoz-Lazo et al. 2019).

In our study system, we suppose that preyed forest invertebrates mainly survive on C_3 forest resources in remnants surrounded by pasture matrix, probably because of their sensitivity to conditions in pastures. This idea is corroborated by Pompermaier et al. (2020), who demonstrated that woodland savanna arthropods feed more on C_3-plant sources in fragments immersed in a pasture matrix, although there is a small consumption of exotic C_4 resources within remnants, and there is a proportional increase in the assimilation of exotic C_4 resources from boundary habitat (savanna-pasture) towards the matrix. However, another study showed the agile opossum can incorporate C_4 invertebrate resources from surrounding native grasslands in fire-degraded forests in the Brazilian Cerrado biome (Ribeiro et al. 2019). This difference in the ability to assimilate C_4 resources from forests surrounding environments might be linked to matrix type and quality, which apparently influences matrix permeability for the studied species under a trophic perspective.

Our results also reveal that *G. agilis* presents high trophic plasticity in these altered landscapes, and feeds on different trophic levels depending on patch size and landscape context. Contrary to our expectations, $\delta^{15}N$ values were similar irrespective of patch size in the most degraded landscape, indicating no changes in trophic position. In eroded landscapes, patches are so isolated from each other that the species-area relation is lost, since populations are exposed to low colonization rates and high extinction rates [e.g. extinction threshold (Andren 1994; Pardini et al. 2010)]. In this sense, if resource organisms (plants and arthropods) experience the effects of the extinction threshold, it could potentially lead to homogeneous resource availability and diversity between patches of different sizes. In fact, landscape simplification can select against more specialized species, leading to functional biotic homogenization in arthropod communities (Gámez-Virués et al. 2015), as well as to taxonomic homogenization of plant communities in tropical forests. This would be a consequence of the proliferation of ecologically-plastic, pioneer, and generalist species across hyper-fragmented landscapes (Lôbo et al. 2011). Consequently, in an extremely simplified and eroded landscape, agile opossum individuals would remain spatially restricted within resident patches to forage on whichever resources there are available inside each patch, given its small home range and low dispersion ability (Ribeiro 2011; Shibuya et al. 2018). If resource biotas are homogenized across patches, it should cascade through the food web

(Wirth et al. 2007), and be reflected in the trophic position of generalist consumers (Layman et al. 2007b).

For both the landscape with intermediate levels of habitat amount and the more conserved one, we found a negative relation of patch size with δ^{15}N values, in accordance with our hypothesis. There was a general pattern of gradual transition from a higher trophic level to a more basal consumer position from small to large patches. This effect was stronger in small patches in the intermediate landscape, where individuals occupied higher trophic positions nearly corresponding to a third-order consumer. However, in larger patches within the more conserved landscape, individuals showed the lowest trophic level, revealing a higher contribution of basal resources to their diet.

Studies with several taxa across different ecosystems show that generalist consumers present shifts in trophic niche and occupy higher trophic positions under conditions of fragmentation or habitat alteration, including predator lizards (Resasco et al. 2018), omnivore bats (Muñoz-Lazo et al. 2019), herbivore geese (Lei et al. 2019), and different guilds of large mammals (Magioli et al. 2019). Drivers to these shifts result from diverse mechanisms: i) a reduction of fruit availability in patches compared to continuous forest leading to higher ingestion of arthropod resources (Muñoz-Lazo et al. 2019); ii) changes in trophic structure of arthropod prey resulting from loss of detritivore prey in patches compared to continuous forests (Resasco et al. 2018); iii) increased intake of high protein animal food sources to supply energy requirements in low quality habitats (Lei et al. 2019); iv) consumption of nitrogen-enriched food items from the agricultural matrix (Magioli et al. 2019).

We can state that the higher trophic position of the agile opossum in smaller patches in the referred landscapes does not result from consumption of nitrogen-enriched items from the matrix, since individuals did not present C_4 pasture signals in their hair, contrary to the findings of Magioli et al. (2019). Thus, we propose that shifts in trophic position potentially result from either a possible change in arthropod trophic structure with patch size and overall reduction of fruit availability with an increase of fragmentation and habitat loss. Fruit availability is lower in forest fragments compared to continuous forests (Terborgh 1986; 1992). If large patches (> 100 ha) are closer to pristine continuous forests in terms of habitat structure and plant diversity, then they should also present higher fruit availability compared to small-sized remnants, as observed in the study area (personal observations, unpublished data, 2018). Fruits are an important food item to *G.*

agilis' diet (Camargo et al. 2014), so it is expected that individuals respond to higher availability of this basal resource, potentially leading to an overall lower trophic position in larger patches, especially within the more conserved landscape.

With lower fruit availability, *Gracilinanus* may increase the consumption of arthropod resources to fulfil energetic, nutritional, and water requirements (Camargo et al. 2014). Thus, in intermediate landscapes, arthropod resources show higher importance to the opossum's diet than more basal resources, especially in smaller patches. With and Pavuk (2011) showed that fragmentation effects on arthropod morphospecies richness were strong at intermediate levels of habitat amount of agricultural landscapes, and it could be linked to greater resource diversity and more favorable microclimates along habitat edges (Crist and Ahern 1999), corroborating the intermediate disturbance hypothesis (With and Pavuk 2011). However, studies evaluating the effects of fragmentation and habitat loss separately suggest that arthropod guilds respond differently to these landscape alterations (mainly by edge mediated effects). Herbivores (from the orders Coleoptera, Hemiptera) are hampered by habitat loss depending on functional group (Rossetti et al. 2014; Gamez-Virués et al. 2015; but see Benítez-Malvido et al. 2016), while omnivorous and specialized predators can benefit either from habitat loss and leaf-cutting ants, from fragmentation (Wirth et al. 2007; Benítez-Malvido et al. 2016; Gámez-Virués et al. 2015). If shifts in the trophic structure of animal resource communities driven by fragmentation and habitat loss should be revealed by variations in the trophic position of a consumer across the gradient of habitat alteration (Layman et al. 2007b; Resasco et al. 2018), then the observed changes in *G. agilis* trophic position across the fragmentation gradient in the intermediate landscape might result from changes in arthropod communities undergoing synergetic effects of fragmentation and habitat loss.

In the most degraded landscape, as predicted by our alternative hypothesis, *G. agilis* showed a slight niche expansion towards smaller patches, but without shifts in ellipse position (ellipses were strongly overlapped). It means the agile opossum fed on the same trophic level irrespective of patch size but incorporated a slightly higher diversity of food items in small patches. Higher trophic diversity in small patches compared to larger ones in this landscape might be explained by the consequences of forager density on diet breadth, as suggested by the optimal foraging theory (OFT). OFT predicts that under low resource availability, because of competition, the range of food items consumed will increase (Emlen 1966; Macarthur and Pianka 1966; Schoener 1971).

This seems to be the case here, since the agile opossum showed higher population density in small patches within the degraded landscape (Fig. 4A – Appendix I), suggesting a high degree of intraspecific competition. Under this condition, individuals may include all potential food items in their diets (Emlen 1966), leading to a broader trophic niche (higher SEAc value, i.e. trophic diversity). This density-dependent effect on niche has been demonstrated for lizards (Roughgarden 1972), flies (Bolnick 2001), and bees (Fontaine et al. 2008).

In the intermediate landscape and in the more conserved one, according to our hypothesis, we observed a progressive niche shift from a more insectivore-omnivore diet towards a more frugivore-omnivore one, associated with niche expansion, from small to large patches, and more pronounced in the more conserved landscape. In other words, we observed a niche collapse with the increase of fragmentation. In these landscapes, forest basal resources (probably fruits) and primary consumer arthropod prey showed a progressive contribution to the diversification of *G. agilis* niche, with the increase in patch size and habitat amount available in the landscape. This pattern of niche shift might be related to changes in forest structure and landscape connectivity following fragmentation and habitat loss [e.g., increased canopy openness and tree mortality, increased density of pioneer plants while old growth species decline in number, increased density of lianas; see Laurence et al. (2000)]. These changes should affect habitat use (Melo et al. 2013; Hannibal et al. 2018), resource exploitation (Klarner et al. 2017; Resasco et al. 2018), resource diversity, and availability (Laurence et al. 2000; Haddad et al. 2015).

Habitat structure influences the occurrence of small mammals (Camargo et al. 2018), and changes in forest complexity and heterogeneity resulting from fragmentation and habitat loss are important determinants of abundance, richness, and species composition of this animal group in fragmented landscapes (Delciellos et al. 2016; Hannibal et al. 2018). Also, microhabitat use leads to isotopic niche space differentiation in small mammals (Dammhahn et al. 2013; Ribeiro 2015b; Galetti et al. 2016). Thus it is expected that enhanced vertical stratification between conspecifics in more complex forests also favors trophic niche partitioning. Camargo et al. (2019) showed that forest structure and resource diversity and availability influences interaction networks of *G. agilis* in the Brazilian savanna. They suggested that more structured forests (thick and spaced trees) increase vertical segregation among individuals, allowing differential resource exploitation between those that use preferentially the ground, and those that use both the ground and the understory strata, leading to higher levels of nestedness (i.e., individuals that use both strata add new food items in relation to those that are more terrestrial). Additionally, fruit abundance and arthropod diversity were related to modularity in the same study, indicating that increasing these resource features enhances diet segregation generating modules of individual-resource interactions (Camargo et al. 2019).

These results based on network interactions corroborate our findings of niche expansion of the agile opossum with increased patch size and habitat amount in the landscape because large patches tend to suffer less from edge effects and thus present more structured, complex forests, especially when there is more habitat amount in the surroundings (Laurance et al. 2018). Thus, there might be higher resource diversity to be explored in different vertical strata [mostly fruits (Laurence et al. 2000); and arthropod primary consumers, within the more conserved landscape (Benítez-Malvido et al. 2016)] compared to small remnants, possibly leading *Gracilinanus* individuals to segregate spatially and thus dietarily between forest strata. Moreover, higher resource diversity and availability could represent chances for individual specialization in certain food items (Bolnick et al. 2003). Consequently, higher spatial segregation and individual specialization should lead to overall niche expansion at the population level.

To our knowledge, this is the first study to evaluate fragmentation effects on trophic niche depending on the context of habitat loss. Our results indicate that habitat amount in the landscape determines the strength of fragmentation effects on niche responses of a small mammal in the Brazilian savanna, supporting the predictions of Fahrig (2013) and other authors who found that the overall habitat amount left in the landscape is an important predictor of biodiversity in human-altered landscapes (Melo et al. 2017; Hannibal et al. 2018). Furthermore, our results show that the consequences of human activities on ecosystems go far beyond species loss, impacting species´ trophic ecology, niche breadth, trophic structure, and habitat use, as also found by other studies (Layman et al. 2007b; Resasco et al. 2018; Magioli et al. 2019; Muñoz-Lazo et al. 2019).

Isotopic analysis of generalist consumers represents unique opportunities for better understanding how key biotic and abiotic processes are altered with landscape fragmentation (Resasco et al. 2018). Species that are tolerant to habitat modification (such as the agile opossum) prove to be good models to evaluate the impacts of fragmentation in gradients of habitat modification on different aspects of a species' ecology (Layman, Quattrochi, et al. 2007; Resasco et al. 2018; Muñoz-Lazo et al. 2019). As they may occur across the complete gradient, it enables researches to fully register and investigate niche shifts patterns, thus revealing ecological changes potentially driven by spatial effects and/or environmental alterations.

In this sense, we were able to record changes in the opossum´s ecological role in the system (e.g., shifts in trophic level) over the fragmentation gradient depending on landscape context of habitat loss. We showed that these human driven alterations have pervasive effects on species trophic ecology. Muñoz-Lazo et al. (2019) showed a similar shift in the ecological role of an omnivore bat in a neotropical forest, reducing the consumption of fruits and enhancing the ingestion of insects in fragments compared to continuous forests. Our study is consistent with this finding, and reinforces that trophic responses to landscape changes can lead omnivore consumers to reduce its role as fruit dispersers, mainly in small fragments, hampering their potential to contribute with the regeneration of altered landscapes (Muñoz-Lazo et al. 2019).

Moreover, we demonstrated that even highly plastic species such as the agile opossum can be strongly dependent on forest resources, even in patches inserted in a severely disrupted landscape (<10% habitat amount). Thus, the present study strengthens the statement that every fragment is important to conservation, even small ones (e.g. <10 ha) (Laurance et al. 2018). Their protection should ensure refugia to surviving forest populations, sources of plant propagules, and may act as stepping-stones in human-modified landscapes (see Laurance et al. 2018). However, we state that the ecological role of a species may be severely hampered in hyper-fragmented landscapes and could affect ecosystem functioning. Finally, the consequences of fragmentation on habitat quality and how it affects consumer trophic ecology remain poorly understood. Thus, we argue that future studies should investigate the direct impacts of changes in the environmental conditions within patches following fragmentation and habitat loss on trophic niche. Additionally, it has been demonstrated that seasonality affects food availability in these ecosystems, influencing changes in trophic niche in small flying and non-flying mammals (Muñoz-Lazo et al. 2019; Ribeiro et al. 2019). Therefore, it might be important in the future to consider the effects of seasonality on trophic niche shifts to better understand the responses of tropical species to landscape changes.

Acknowledgements

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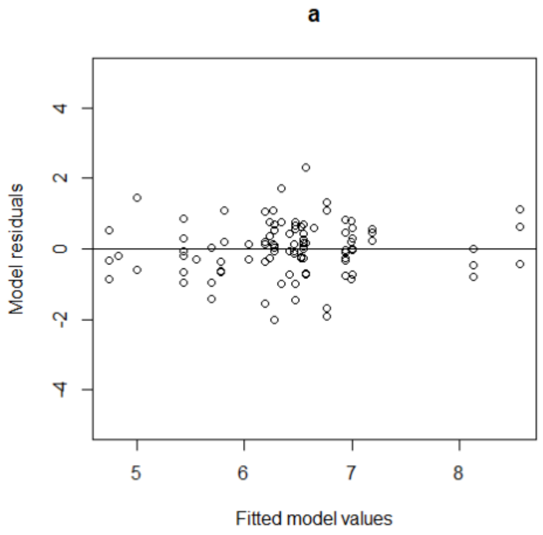
Appendix I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-2
-4
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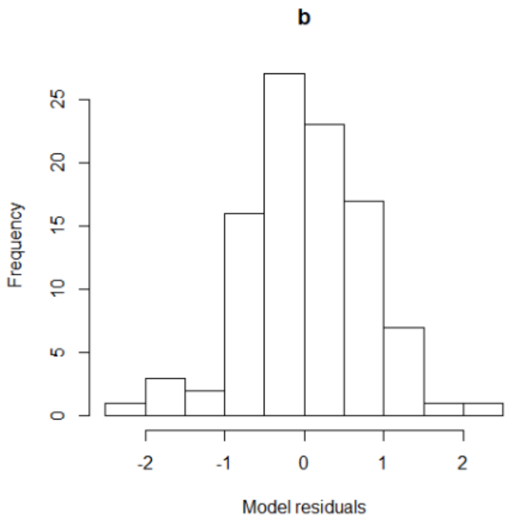
6
7
8
Fitted model values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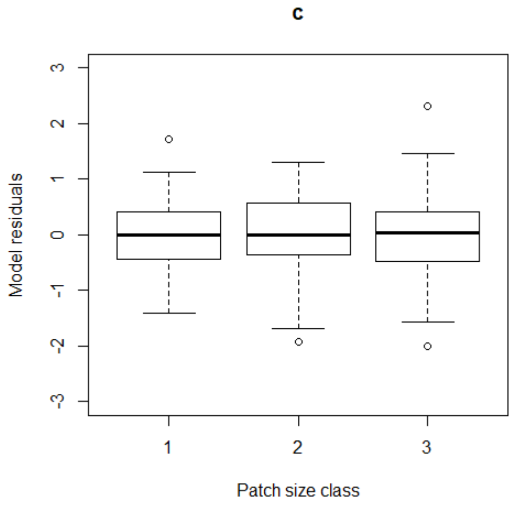
Model residuals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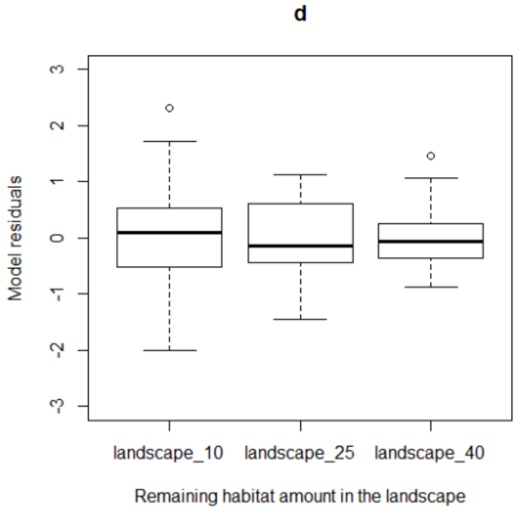
1
2
3
Patch size class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-2
-3
landscape_10
landscape_25
landscape_40
Remaining habitat amount in the landscape

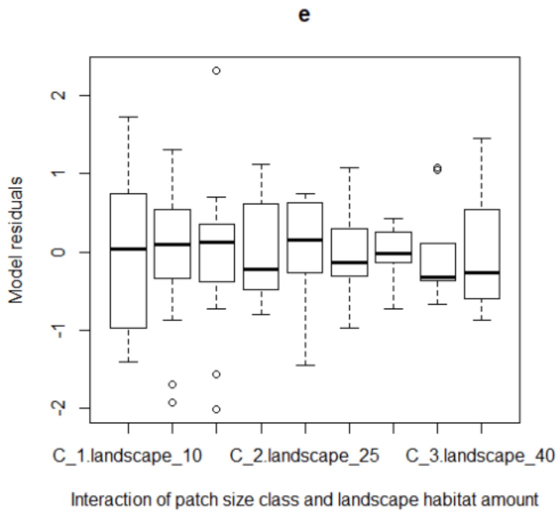
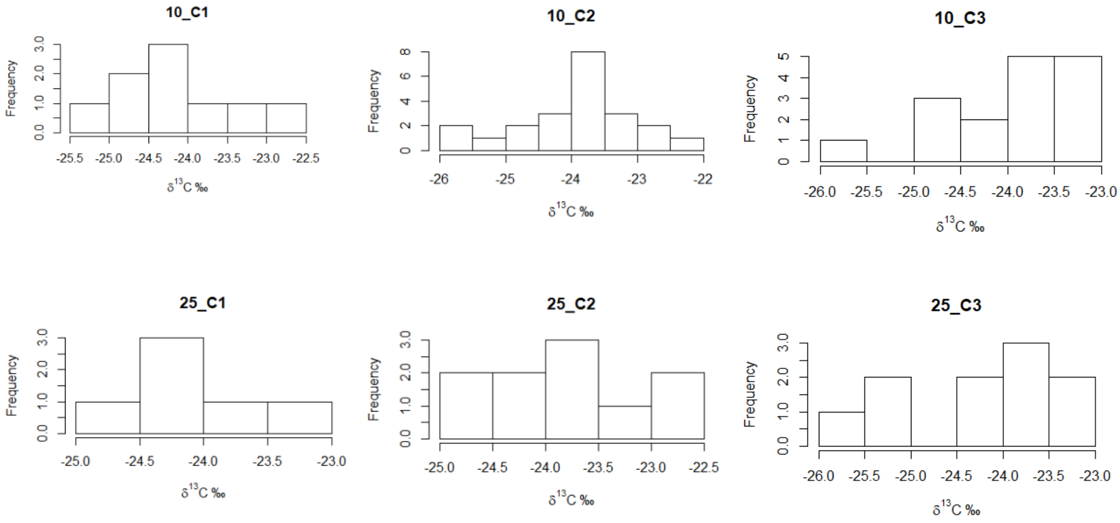


Figure 1A. Validation of the final linear mixed model describing the effects of habitat fragmentation and habitat loss on δ^{15}N values of the agile opossum *Gracilinanus agilis* hair content (Deviance = 242.8; χ^2= 37.295; df =8; p-value < 0.0001). Visual inspection of residuals following Zuur et al. (2009). (a) Model residuals versus fitted values; (b) Histogram of model residuals; (c) Model residuals versus explanatory variables patch size class, and (d) habitat amount in the landscape and interaction terms (e).



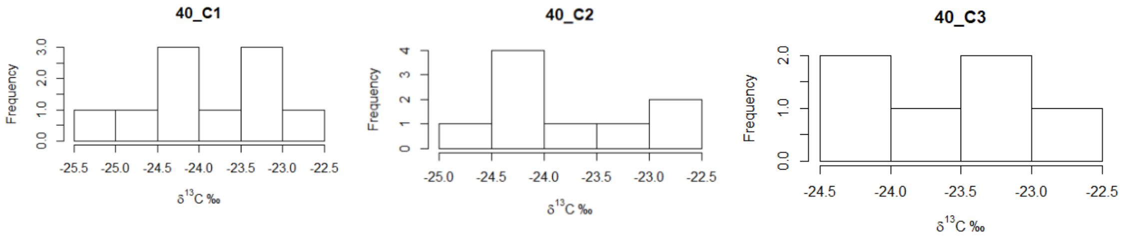


Figure 2A. Histograms of δ^{13}C values of hair samples from *Gracilinanus agilis* distributed by patch size classes (C1- class 1, C2 – class 2, C3 – class 3) within landscapes with different remnant habitat amount (10, 25, 40% of natural cover) in semideciduous forests in the Brazilian Cerrado.

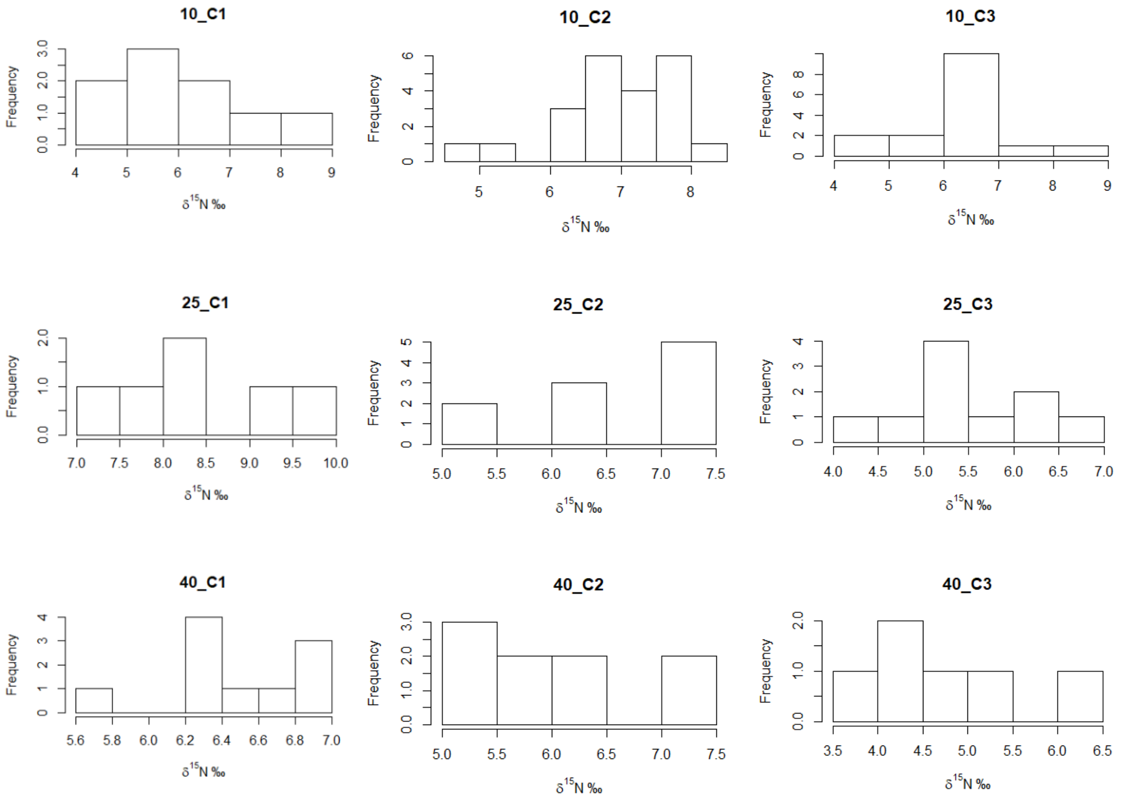


Figure 3A. Histograms of δ^{15}N values of hair samples from *Gracilinanus agilis* distributed by patch size classes (C1- class 1, C2 – class 2, C3 – class 3) within landscapes with different remnant habitat amount (10, 25, 40% of natural cover) in semideciduous forests in the Brazilian Cerrado.

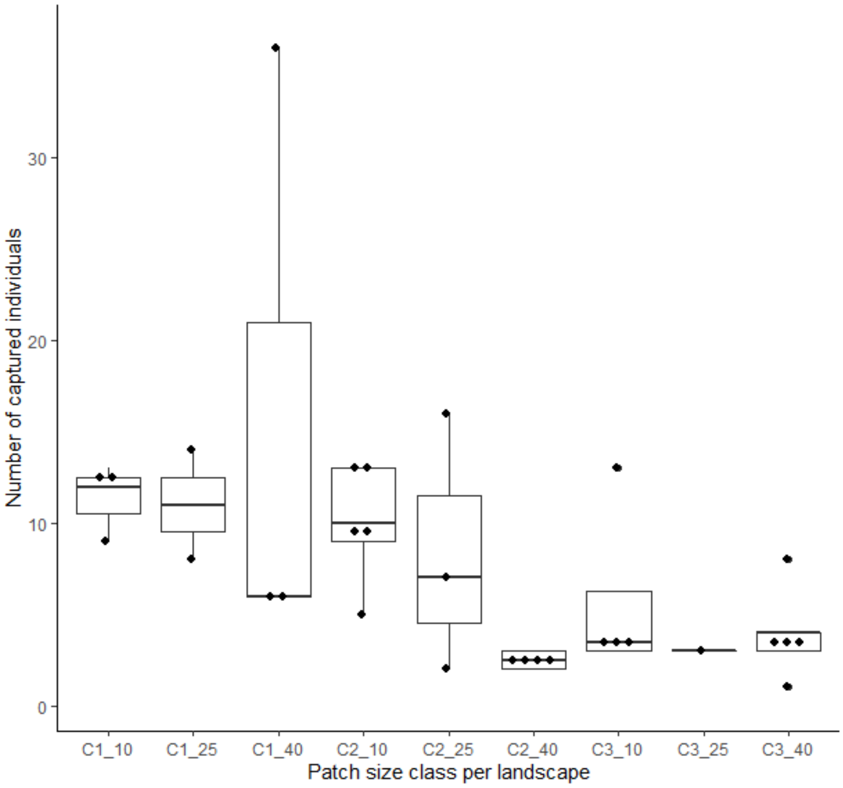


Figure 4A. Number of captured individuals (*Gracilinanus agilis*) in patch size classes (C1- class 1, C2 – class 2, C3 – class 3) within landscapes with different remnant habitat amount (10, 25, 40% of natural cover) in semideciduous forests in the Brazilian Cerrado.

Table 1A. Significance of global linear mixed models of the effects of habitat fragmentation and habitat loss on δ^{13}C and δ^{15}N hair content values of the agile opossum *Gracilinanus agilis*. The significance of the model was determined by changes in deviance and p-values generated by comparing global models against null models.

Global model		**df**	**Deviance**	χ^2	**p-value**
	Variables				
δ^{13}C	Patch size class x Landscape	8	212.89	4.879	0.770
δ^{15}N	Patch size class x Landscape	8	242.80	37.295	**1.016 x 10^{-5}**

Table 2A. Linear mixed model estimated parameters and standard error (SE) for the relative effects of patch size and habitat loss (landscape habitat amount) on δ^{15}N values of the agile opossum *Gracilinanus agilis* in semideciduous forests in the Brazilian Cerrado.

Fixed effects	Parameter	Estimate	SE
Intercept	β0	6.0933	0.3393
Patch size class 2	β2	0.8858	0.4137
Patch size class 3	β3	0.3047	0.4344
Landscape 25 %	β4	2.2550	0.5365
Landscape 40 %	β5	0.3864	0.4724
Patch size class 2: Landscape 25 %	β6	-2.6840	0.6778
Patch size class 3: Landscape 25 %	β7	-3.0530	0.6966
Patch size class 2: Landscape 40 %	β8	-1.2949	0.6207
Patch size class 3: Landscape 40 %	β9	-1.9274	0.6746
Random Effect			
Intercept	υ	0.1166	0.3415
Residual		0.6864	0.8285

Capítulo 3

The effects of habitat quality and spatial scales in the isotopic niche space of a didelphid opossum in fragmented landscapes in a neotropical savanna

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Abstract

Studies investigating fragmentation consequences on animal trophic ecology have focused on the effects of either patch size and/or habitat loss as the main drivers of species responses, while the effects of habitat quality have been underestimated or poorly studied compared to spatial scales. Here we investigated how habitat quality (evaluated as forest structure and food resources), patch characteristics, and landscape structure influence the isotopic niche space of the didelphid agile opossum *Gracilinanus agilis* in fragmented landscapes of semideciduous forests in the Brazilian savanna. We adopted a multiscale approach to better comprehend the species´ trophic responses to these complex environmental changes. We livetraped small mammals, measured habitat quality descriptors, as well as patch and landscape metrics (in a 1 km buffer) in 36 forest patches during the year 2018 between the rainy-dry season (April-June), and the dry-rainy season (August-October). We calculated isotopic niche space metrics based on ratios of δ^{13}C and δ^{15}N of hair samples. Regression analyses indicated that the variation in δ^{13}C range (CR) was not explained by any of the evaluated habitat or spatial scales. On the other hand, δ^{15}N range (NR) was affected at the patch scale, revealing a positive effect of patch core area, which indicates that opossum individuals assimilated more trophic levels in larger and more conserved patches than in smaller ones. Moreover, trophic diversity (SEAc) was not influenced by the evaluated predictors at any scale. Finally, niche uniformity (SDNND) was the only isotopic niche space metric that responded to different scales: as a function of habitat quality (in both dimensions of forest structure and food resources), this metric was negatively influenced by the number of vines (indicating that more altered forests led individuals to converge in trophic niche); also negatively affected by the abundance of Isoptera insects (termites), indicating that the more abundant termites were, the more equally individuals within a population tended to include this food item in their diets; lastly, at the patch scale, SDNND showed a positive effect of patch core area, revealing that larger patches with more pristine vegetation promotes intraspecific niche partitioning within each population. Our results show that different aspects of trophic ecology respond diversely to distinct scales, but responses to patch or/and habitat quality features prevailed over the landscape scale, indicating that smaller scales might be more important to determine changes in trophic niche space of *G. agilis*, probably because this small bodied species responds to finer grain environmental changes. In this sense, we emphasize the need to evaluate the impacts of changes in habitat quality, a usually neglected aspect of fragmentation effects in ecological research.

Keywords: Cerrado, stable isotopes, forest structure, food resources, trophic niche

Introduction

Fragmentation and habitat loss are responsible for biodiversity declines and alterations in ecological processes worldwide (Fahrig 2003; Estes et al. 2011; Haddad et al. 2015). Reduction in patch area, increased isolation, increased edge effects, and alterations in habitat quality (i.e., habitat suitability for a given species) lead to pervasive consequences in ecosystem dynamics, going through changes in species abundance, diversity, and composition, toward modifications in trophic dynamics (Melián and Bascompte 2002; Haddad et al. 2015; Honorato et al. 2015).

Studies investigating the consequences of fragmentation on animal trophic ecology have focused on the effects of either patch size and/or habitat loss as the main drivers of species responses (Post et al. 2000; Layman et al. 2007b; Reuter et al. 2016; Korotkevich et al. 2018; Resasco et al. 2018; Magioli et al. 2019; Muñoz-Lazo et al. 2019), while the effects of habitat quality have been underestimated (Mortelliti et al. 2010) or poorly studied compared to spatial scales (Navarro-López and Fargallo 2015; Lei et al. 2019). However, these responses may result from a synergistic relationship between patch characteristics, landscape context, and habitat quality (Mortelliti et al. 2010; Didham et al. 2012). Therefore, adopting a multiscale approach to explore the impacts of landscape conversion on trophic relations should allow a more complete overview of the ecological mechanisms driving a species capability to survive in such altered environments, which is fundamental to underpin accurate conservation policies in fragmented landscapes. Although interest in this topic has been increasing to evaluate changes in species occurrence and occupancy (Mendes et al. 2017; Bhakti et al. 2018; Hannibal et al. 2018), studies evaluating aspects of trophic ecology under a multiscale approach are still lacking.

The relative effects of habitat quality, patch, and landscape characteristics on trophic ecology should depend on the scale at which species perceive and respond to environmental complexity and heterogeneity, which is linked to ecological traits such as resource requirements, body size, dispersal ability, habitat preferences, trophic level, and trophic plasticity (Chapter II, With 1994; Honorato et al. 2015; Keinath et al. 2017; Mendes et al. 2017; Magioli et al. 2019). Regarding small mammals, diverse habitat characteristics related to forest structure (e.g., lianas, fallen logs, understory density, litter volume, canopy cover, tree diameter), and food resources (e.g., fruit abundance, arthropod diversity), patch and landscapes features (e.g., patch area, normalized difference vegetation index - NDVI, isolation, and habitat amount) are known to influence diversity, abundance, species composition, and trophic aspects of their ecology (Chapter II, Pardini et al. 2010; Delciellos et al. 2016; Galetti et al. 2016; Melo et al. 2017; Hannibal et al. 2018; Camargo et al. 2019; Ribeiro et al. 2019).

Aspects of animal trophic ecology have been increasingly studied with stable isotopes, on the basis of isotopic niche, an *n*-dimensional hypervolume (where *n* is the number of isotopes) occupied by a population in delta space (Boecklen et al. 2011; Shipley and Matich 2020). Studies on food web ecology and land-use change typically use stable isotopes of carbon (^{13}C) and nitrogen (^{15}N) (Layman et al. 2012; Resasco et al. 2018; Magioli et al. 2019). Isotopic carbon ratio ($\delta^{13}C$) relates to basal resources assimilated by consumers, varying significantly among primary producers with different photosynthetic pathways (e.g., C_3 trees and shrubs, and C_4 grasses), and thus providing traces on habitat use (Layman et al. 2007a; Ben-David and Flaherty 2012; Magioli et al. 2019; Ribeiro et al. 2019). Ratios of nitrogen isotopes ($\delta^{15}N$) present stepwise enrichment with trophic transfers, serving as an indicator of trophic level within a food web (Post 2002; Ben-David and Flaherty 2012).

Here we investigated how habitat quality (evaluated as forest structure and food resources), patch characteristics, and landscape structure influence the isotopic niche space of the didelphid agile opossum *Gracilinanus agilis* (Burmeister, 1854) in fragmented landscapes of semideciduous forests in the Brazilian savanna. We adopted a multiscale approach to better understand the species´ trophic responses to these complex environmental changes. At the habitat scale, we expected that this arboreal-scansorial marsupial might respond to variations in habitat quality since forest structure complexity influences the availability of spatial resources that can be explored by individuals in search for food, besides influencing availability and diversity of food items. So, we predicted a positive effect of canopy cover, tree height and basal area on isotopic niche area (i.e., niche diversity), $\delta^{15}N$ range, and niche uniformity, since those habitat characteristics are related to higher complexity, providing opportunities of exploring diverse resources in different forest strata (Camargo et al. 2019a). On the other hand, we foresaw a negative effect of vines on those niche metrics, because these plants are usually linked to severely altered forests and edge effects, habitat conditions which might hold fewer resource diversity (Campbell et al. 2018). Regarding $\delta^{13}C$ range, we also expected a negative effect of canopy cover, tree height and basal area, but a positive effect of vines, because in more altered forests the agile opossum might assimilate C_4 resources from the matrix, widening the $\delta^{13}C$ dimension of niche (Magioli et al. 2019; Ribeiro et al. 2019; Pompermaier et al. 2020). In relation to food resources, we expected arthropod diversity and fruit availability to be the main drivers of changes in isotopic niche space metrics, since these resources influence small mammal guild occurrence (Hannibal et al. 2020), isotopic trophic niche (Chapter II, Ribeiro et al. 2019), and network interaction metrics of the agile opossum (Camargo et al. 2019a).

At the patch scale, we expect both patch size and forest density (NDVI) to be important variables to influence isotopic niche space, positively affecting niche area (i.e., niche diversity) and $\delta^{15}N$ range, and niche uniformity, while negatively relating to $\delta^{13}C$ range. Patch size influences isotopic niche space for many taxa (Chapter II, Resasco et al. 2018; Muñoz-Lazo et al. 2019), and NDVI – a proxy for forest integrity (Cabacinha and de Castro 2009) – has been identified as an important determinant of small mammal composition in semideciduous forests (Hannibal et al. 2018). Finally, at the landscape scale, we predicted a positive effect of habitat amount on isotopic niche area (i.e., diversity), $\delta^{15}N$ range, and niche uniformity, but a negative effect on $\delta^{13}C$ range. Habitat amount is an important driver of changes in isotopic niche space (Chapter II, Reuter et al. 2016), species richness, diversity (for anurans, Almeida-Gomes et al. 2019; birds, De Camargo et al. 2018; and small mammals, Melo et al. 2017), and mammal species composition (Pardini et al. 2010; Garmendia et al. 2013; Arroyo-Rodríguez et al. 2016; Hannibal et al. 2018).

Materials and Methods

Study area

The study was conducted in 36 patches of semideciduous seasonal forests, ranging from 2 to 760 ha, in a highly deforested portion of the Brazilian Cerrado. These sites were located in the municipalities of Abadiânia (16º2´51´´ S 48º51´44´´ W), Jesúpolis (15°57´05´´ S 49°22´26´´ W), Jaraguá (15º44´31´´ S 49º20´6´´ W), Ouro Verde de Goiás (16°13´13´´ S 49°11´36´´ W), Pirenópolis (15°53´06.40´´ S 49°10´46.29´´ W), and São Francisco de Goiás (15º55´51´´ S 49º15´2´´ W), in the central portion of the state of Goiás, Brazil. In these regions, the matrix is composed mainly of pasture, but there are also agricultural areas (such as crop fields and/or banana plantations), and few natural patches of savanna vegetation (Figure 1). Sampling sites were located in the Legal Reserves of private farms, which are the natural vegetation area all landowners are legally obliged to preserve. The climate is classified as Aw according to Köppen, with two well defined climatic seasons (hot/wet summers from October to March, and dry/cold winters from April to September).

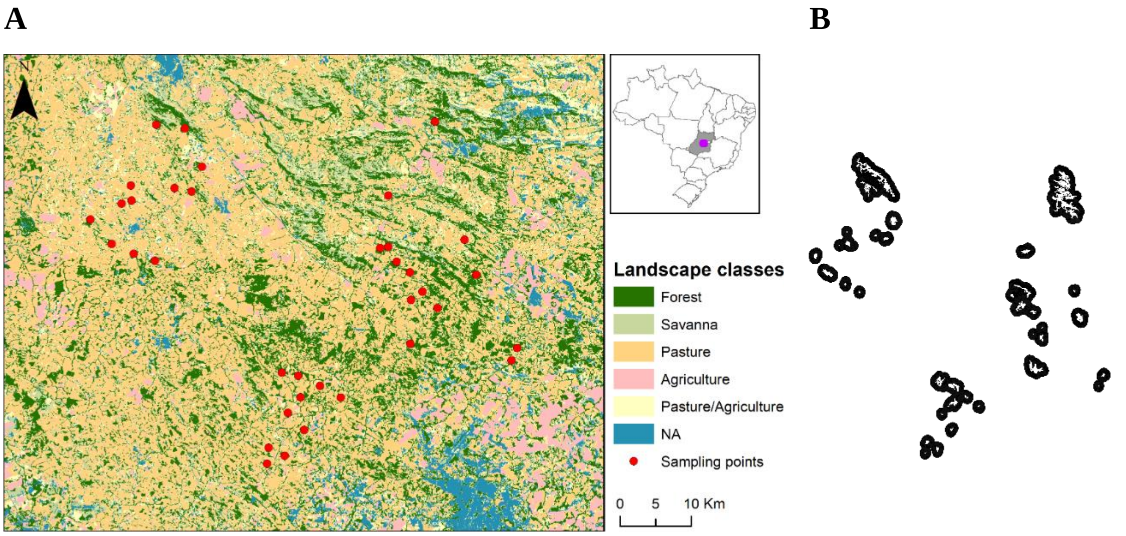

Figure 1. (A) Sampling patches (red dots) in central Goiás state, Brazil (highlighted in grey in the inset map). (B) Buffer of 1-km radius around patch borders used to estimate landscape metrics.

Studied species

The agile opossum *Gracilinanus agilis* (Burmeister, 1854) is a small bodied (20-30 g), solitary, nocturnal, didelphid marsupial with arboreal and scansorial habits (Emmons and Feer 1997). It feeds mostly on arthropods (mainly Hymenoptera, Isoptera, Hemiptera, and Coleoptera), small fruits, and occasionally birds (Camargo et al. 2014). Also, its diet varies seasonally: reproductive females feed more heavily on insects during the mating season (Camargo et al. 2014). Stable isotope evaluation of *G. agilis* confirmed a high arthropod consumption, revealing that forest-resident individuals can switch between prey resources from forests (C_3) in the rainy season to grasslands (C_4) in the dry season (Ribeiro et al. 2019). Reproduction occurs seasonally, from the end of the cool-dry season to mid/end of the warm-wet season (Lopes and Leiner 2015). This marsupial is widely distributed in South America, ranging over the east of the Andes in Peru, Bolivia, Paraguay, Uruguay, and Argentina (Emmons and Feer 1997). In Brazil, it inhabits the Cerrado, Caatinga, and Pantanal biomes (Paglia et al. 2012), occurring in forest formations, e.g. gallery forests, dry forests, and woodland savannas (Vieira and Palma 2005).

Small mammal survey

In each of the 36 sampled patches, we established a trapping line of 200 m, located 30 m from patch edges to minimize edge effects. Each line had 20 trap stations, placed every 10 m, with four livetraps each, where half were set on the ground, and half in the understory (at least 1.5 m height). Every station had a Tomahawk®(300 x 160 x 160 mm) and a small Sherman® (250 x 80 x 90 mm) on the ground, and a big Sherman (300 x 80 x 90 mm) and a small one in the understory, except for the first and last trap stations, where we replaced a Tomahawk trap by a big Sherman. The study was conducted over the year 2018 between the rainy-dry season (April-June) and the dry-rainy season (August-October), thus encompassing seasonal variations in diet. Captures occurred during four consecutive nights per field campaign, resulting in an effort of 640 trap-nights per patch and 23,040 trap-nights in total.

Traps were baited with a mixture of peanut butter, corn powder, sardine, and banana. Captured animals were identified, marked with numbered ear-tags, measured and weighted. We also recorded age (following Macedo et al. 2006), gender, and reproductive status. We collected a hair sample from the posterior dorsal region from all individuals with a clean scissor, and stored samples in plastic tubes. Animals were released in the same trap location where they were captured. Voucher specimens were collected and held in the Mammal Collection of the Department of Zoology, University of Brasília (UnB, Brasília, Brazil). All procedures followed the guidelines of the American Society of Mammalogists for the use of wild animals in research (Sikes et al. 2016). We conducted the study with the permission of the Committee of Ethics and Animal Use from the University of Brasília (28/2018), Instituto Chico Mendes de Biodiversidade (SISBIO 61990), and Secretaria de Meio Ambiente do Estado de Goiás (SECIMA/CEMan 006/2019).

Habitat quality

Here we considered patch quality as properties of the habitat that might have an impact on population parameters such as survival and fecundity (Mortelliti et al. 2010). To evaluate habitat scale and habitat quality, we chose environmental variables revealed as important to small mammals´ occurrence, habitat use, and foraging, that can potentially affect population parameters and individual condition (Pardini et al. 2005; Ribeiro 2015a; Delciellos et al. 2016, 2018; Camargo et al. 2018; Hannibal et al. 2018, 2020; Ribeiro et al. 2019). These variables describe habitat heterogeneity, forest complexity, and food resource availability.

We sampled descriptors of habitat quality in ten 4 x 4-m plots located every even trap station along the transect line in all patches. To evaluate forest structure, we measured the following variables inside each plot: 1) canopy cover, as the proportion of closed pixels from a photograph (one per plot, and used mean values per patch) taken with a digital camera in the center of each plot, using the software image J. We took one picture per season and used mean values; 2) mean number of vines; 3) mean tree height (m) of the closest four trees from the plot center, with circumference $\geq$ 16 cm at 30 cm height - estimated with a 3 m pole; 4) basal area, estimated from the diameter at breast height (DBH) from the same four previously measured trees; 5) understory clutter (to 3 m height) (%), estimated with a graduated 3 m pole (with a graduation of 10 cm) following Martins et al. (2017); 6) litter volume (cm^3), estimated from litter material sampled in a 50 x 50-cm quadrat inside each plot (located in its superior left corner), following Santos Filho et al. (2008a). We placed the collected litter inside a translucid graduated cylindric box (with 28.2 cm diameter) and pressed down the material with a 1 kg cover, which indicated the correspondent litter height in a coupled scale of 120 mm (Figure 2). Litter height (h) was then used to estimate cylinder volume according to $V = \pi. (14.1)^2.h$.

Since cattle ranching is the main human activity in the study regions, we also estimated 7) cattle intrusion to measure human-use habitat modification in forests. We classified intrusion level as an ordinated variable (0-4) based on incidence of footprints, cattle trampling and feces in a 15-m radius around each plot´s center. For this variable we used median plot values for each patch as the sample unit, while we used mean values for the other variables.

To estimate food availability, we directly counted total number of zoochorous fruits in the understory (to 3 m height) [or estimated it according to Chapman et al. (1992)] inside each plot during small mammal sampling. To evaluate arthropod abundance, we used pitfall traps (one per plot, totaling 10 traps per sampling patch), composed of a 500-mL plastic cup containing a solution of water, salt, and detergent. Traps remained opened during four days per sampling period. We estimated arthropod abundance by taxonomic order. However, further analyses included: abundance of the most commonly found orders in *G. agilis* diet (Coleoptera, Hemiptera, Hymenoptera, and Isoptera, Camargo et al. 2014); and arthropod diversity, estimated with Shannon Index (Exp [H´]; Jost 2006), based on all orders registered.

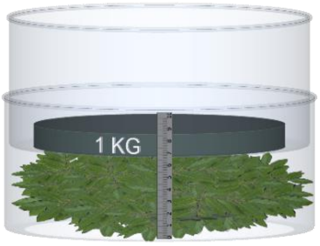

Figure 2. Graduated cylindric box used to estimate litter volume.

Patch scale

We estimated four metrics for each sampled patch: 1) patch area (m^2); 2) patch core area (m^2), corresponding to patch area minus edge length (50 m), representing a more intact portion of the patch, i.e., lower edge effect for small mammals (Santos-Filho et al. 2008b); 3) patch perimeter (m); 4) NDVI, estimated with Landsat 8 imagery in Google Earth Engine from mean values between dry and rainy seasons of the year 2018. This metric indicates vegetation density, which has been associated with small mammal composition in the Brazilian Cerrado (Melo 2015; Hannibal et al. 2018), and might indicate forest quality.

Landscape scale

To estimate landscape metrics, we selected a buffer of 1-km radius around each patch border (Fig.1). This distance covers the home range size of *G. agilis* (Ribeiro 2011; Shibuya et al. 2018), and is the largest buffer size that avoided overlap with buffers from neighboring focal patches (Hannibal et al. 2018). We calculated the following metrics of landscape structure inside each buffer: 1) mean patch isolation (MNN), as mean distance to all patches (m) (Vieira et al. 2018); 2) mean perimeter-area ratio (MPAR), estimated as the sum of each patch perimeter/area ratio divided by the number of patches, which is a measure of shape complexity; 3) total core area (TCA), estimated as the sum of all patch core areas inside the buffer, and we used it as a measure of habitat amount in the landscape (m^2); 4) total core area index (TCAI), a measure of the amount of core area in the landscape, is a proportion of core area in the entire landscape, equaling zero when no patches in the landscape contain core, and approaches one as the relative proportion of core area in the landscape increases.

Patch and landscape metrics were based on the 2018 land use and land cover map from the MapBiomas project, collection 4.1, which classifies Landsat 8 satellite imagery at a 30-m resolution. Landscape choice was based on the proportion of five land use classes: forest, savanna, agriculture, pasture, and mosaic of agriculture and pasture [see MapBiomas class descriptions in (http://mapbiomas.org)]. Patch (except for NDVI) and landscape metrics were calculated using the Patch Analyst extension in ArcGIS 10.4. All these predictors can influence abundance, richness, as well as species composition for small mammals (Pardini et al. 2005; Delciellos et al. 2016; Vieira et al. 2018).

Isotopic analysis

We collected hair samples from at least three individuals of *Gracilinanus agilis* per patch. In addition, to avoid bias in isotopic values we excluded samples from four patches that were surrounded by soy or banana plantations, since our focus was on the most prevalent pasture matrix. In addition, we tried to equally distribute samples among sexes, and excluded juveniles to avoid possible bias in isotopic values due to gender and age differences in trophic niche. Hair samples were washed with distilled water, subsequently immersed in a 2:1 solution of chloroform and methanol for 30 min, and washed again with distilled water. Afterwards, samples were oven-dried for 12 hours at 65°, shredded and weighted (minimum aliquot of 1.5 mg) in tin capsules on an analytical scale (0.001 g precision) (Ribeiro et al. 2019).

Isotopic analyses were performed at the Stable Isotope Facility of the University of California (SIF), Davis, USA. Samples were analyzed for ^{13}C and ^{15}N isotopes using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). During analysis, samples were interspersed with several replicates of at least four different laboratory reference materials. These reference materials have been previously calibrated against international reference materials, including IAEA-600, USGS-40, USGS-41, USGS-42, USGS-43, USGS-61, USGS-64, and USGS-65 reference materials. A sample’s provisional isotope ratio is measured relative to a reference gas peak analyzed with each sample. These provisional values are finalized by correcting the values for the entire batch based on the known values of the included laboratory reference materials. The long-term standard deviation is 0.2 per mil for ^{13}C and 0.3 per mil for ^{15}N.

The results were expressed in delta notation (δ), in parts per thousand (‰), based on internationally recognized standards. We used the following equation: $\delta\,^{15}$N or $\delta\,^{13}$C (‰) = ($R_{sample} - R_{standard}$) / $R_{standard} \times$ 1.000), where R_{sample} and $R_{standard}$ represent the heavy/light isotope molar ratio of the sample and standard, respectively. The standard used for carbon analysis was Vienna Pee Dee Belemite (Vienna PDB; ^{13}C:^{12}C ratio = 0.01118), and the standard used for nitrogen analysis was atmospheric air (^{15}N:^{14}N ratio = 0.0036765).

Data analyses

Isotopic niche space

Isotopic niche metrics were based on mean values of δ^{13}C – δ^{15}N from *G. agilis* individuals dispersed in isotopic niche space, represented by a biplot. These metrics reveal important aspects of trophic structure and are related to trophic diversity (Layman et al. 2007a; Jackson et al. 2011). To investigate changes in isotopic niche space of the agile opossum, we calculated the following metrics: 1) δ^{13}C range (CR), indicating the variety of basal resources assimilated by the species; 2) δ^{15}N range (NR), which provides information on the diversity of trophic levels assimilated by the species; 3) standard ellipse area corrected for small sample size (SEAc), which is a bivariate standard deviation that represents the core isotopic niche space of a population (Jackson et al. 2011); 4) standard deviation of the mean nearest neighbor distance (SDNND), which is a measure of trophic niche uniformity between individuals of a population in the biplot δ^{13}C - δ^{15}N. Smaller values indicate higher trophic similarity (Layman et al. 2007a; Jackson et al. 2011). These metrics were estimated in R software version 3.6.2 (R Core Team 2019) using the *SIBER* package (Jackson et al. 2011).

Statistical analyses

We used linear models (LM) or generalized linear models (GLM) to evaluate the effects of habitat quality (separately habitat structure and food resources) and spatial scale (patch and landscape) on isotopic niche space metrics. GLMs were used with Gamma distribution whenever needed to accommodate normality deviations of the global model's residuals (Zuur et al. 2009). So, we fitted 16 models in total to investigate these relationships in each dimension (Table 1). To determine which variables were most important to influence response variables at each scale, we compared nested models in a stepwise approach with likelihood ratio tests (LRT). The significance of explanatory variables was given by p-values (based on F tests) for LM, while for GLM it was given by changes in Deviance and p-values (based on χ^2 test). First, we tested for spatial autocorrelation in response variables with Moran´s I. Also, we checked for multicollinearity between predictors with Pearson correlation coefficients (excluding those with $r > 0.5$). During model fitting, we transformed predictors [to $\log_{10}(x)$ or $\log_{10}(x+1)$] in some cases to improve homoscedasticity of residuals (Tab. 1) (Zuur et al. 2007). Additionally, predictors were standardized (scaled to the z-score) to ensure variables had the same scale (Table 2). We tested for overdispersion with Pearson residuals in GLM models. We conducted analyses in R version 3.6.2 (R Core Team 2019), and performed model validation following Zuur et al. (2009).

Table 1. Structure of regression models evaluating the influence of habitat quality (forest structure and food resources) and spatial scale (patch and landscape) on isotopic niche space (Layman et al. 2007a; Jackson et al. 2011) of *Gracilinanus agilis* in the Brazilian Savanna in a fragmented landscape. Response variables: CR – δ^{13}C range; NR – δ^{15}N range; SEAc – standard ellipse area corrected for small sample size; SDNND – standard deviation of the mean nearest neighbor distance. Explanatory variables are grouped into descriptors of habitat quality (forest structure: Height – tree height (m); Vines – mean number of vines; B_area – basal area (m^2); Understory – understory clutter (%); Canopy – canopy cover (%); Litter – litter volume (m^3); food resources: Fruits – total number of fruits; H´_arth – Shannon Index of arthropod diversity; Coleoptera – Coleoptera abundance; Hemiptera – Hemiptera abundance; Isoptera – Isoptera abundance), and spatial scales (patch: Core area (m^2) – patch area excluding 50-m edges; NDVI – vegetation density index accounted for mean values between dry and rainy seasons; and, landscape: MPAR – mean perimeter-area ratio, indicating shape complexity; MNN – mean nearest neighbor distance, indicating mean patch isolation; TCA_m^2 – total core area (m^2) in a 1-km buffer around focal patch).

	Global models
Regression type	**Habitat quality (forest structure)**
GLM	CR ~ Vines + Height + Canopy + Litter + log$_{10}$(B_area) + Understory
GLM	NR ~ Vines + Height + Canopy + Litter + B_area + Understory
GLM	SEAc ~ Vines + Height + Canopy + Litter + log$_{10}$(B_area) + Understory
GLM	SDNND ~ Vines + Height + Canopy + Litter + log$_{10}$(B_area) + Understory
	Habitat quality (food resources)
LM	CR ~ H´arth+ Hemiptera + Isoptera + Coleoptera + Fruits
GLM	NR ~ H´arth+ log$_{10}$(x+1) Hemiptera + log$_{10}$(x+1) Isoptera + log$_{10}$(x+1) Coleoptera + log$_{10}$(x+1) Fruits
GLM	SEAc ~ H´arth+ log$_{10}$(x+1) Hemiptera + log$_{10}$(x+1) Isoptera + log$_{10}$(x+1) Coleoptera + log$_{10}$(x+1) Fruits

GLM	SDNND ~ H´arth+ $\log_{10}$(x+1) Hemiptera + $\log_{10}$(x+1) Isoptera + $\log_{10}$(x+1) Coleoptera + $\log_{10}$(x+1) Fruits
	Patch scale
LM	CR ~ Core area + NDVI
LM	NR ~ Core area + NDVI
GLM	SEAc ~ Core area + NDVI
GLM	SDNND ~ Core area + NDVI
	Landscape scale
LM	CR ~ MNN + TCA + MPAR
LM	NR ~ MNN + TCA + MPAR
GLM	SEAc ~ MNN + TCA + MPAR
GLM	SDNND ~ MNN + TCA + MPAR

Results

We analyzed 85 samples from individuals captured in 22 of the 36 sampled patch sites. Mean sample size per patch was 3.86 (ranging from 3 to 7 hair samples). Mean δ^{13}C value was -24.03 ‰, ranging from -25.07 to -23.46 ‰, which corresponds mostly to assimilation of forest basal resources (C_3) and no matrix resources. Mean δ^{15}N value was 6.50 ‰, ranging from 4.52 to 9.00 ‰. These values suggest an omnivore-insectivore diet with wide trophic plasticity, indicating the agile opossum feeds on basal resources (probably fruits) up to three trophic levels.

We found no spatial autocorrelation in the response variables, according to Moran´s I test (δ^{13}C range: $p = 0.406$; δ^{15}N range: $p = 0.900$; SEAc: $p = 0.406$; SDNND: $p = 0.607$). To avoid multicollinearity, we excluded the following variables to fit models, based on Pearson correlations ($r > 0.5$): level of cattle intrusion (that was highly negatively correlated with understory clutter), Hymenoptera abundance (correlated with Coleoptera abundance), patch area (correlated with patch core area), patch perimeter (correlated with patch area and patch core area), total core area index (correlated with total core area) (Figure AI). Finally, we found no overdispersion in model residuals during GLM fitting.

Regression analyses indicated that variation in δ^{13}C range (CR) was not explained by habitat quality (either forest structure or food resources), patch or landscape scales

(Table AI). Regarding δ^{15}N range (NR), variation was explained only by patch scale, revealing a positive effect of patch core area ($\beta_{\text{core area}}$ = 0.388 ± 0.175; df = 20; t = 2.222, p = 0.038; Figure 3a, (Tab. AI), which indicates that opossum individuals assimilated more trophic levels in larger and more conserved patches than in smaller ones. Moreover, standard ellipse area, or trophic diversity (SEAc), was not influenced by the evaluated predictors at any scale (Tab. AI). Finally, niche uniformity (SDNND) was the only isotopic niche space metric that responded to different scales: as a function of habitat quality (in both dimensions of forest structure and food resources), this metric was negatively influenced by the number of vines (β_{vines} = -0.519 ± 0.162; df = 20; Deviance = 14.870; χ^2 = -4.848; p = 0.002, Fig. 3b, Tab. AI), also negatively affected by the abundance of Isoptera insects (termites) ($\beta_{\text{Isoptera abundance}}$ = -0.542 ± 0.152; df = 20; Deviance = 13.536; χ^2 = -6.182; p = 0.0004, Fig.3c, Tab. AI); at the patch scale, SDNND showed a positive effect of patch core area ($\beta_{\text{core area}}$ = 0.337 ±0.181; df = 20; Deviance = 19.718; χ^2 = -2.693; p = 0.047, Fig. 3d, Tab. AI).

Table 2. Mean and range of response variables (isotopic niche space metrics), and explanatory variables tested in the analyses to predict the influence of habitat quality, patch and landscape scales on isotopic niche space of *Gracilinanus agilis* in fragmented landscapes in the Brazilian Savanna.

Response variable	**Mean [Range]**
δ^{13}C range	1.32 [0.14 – 2.75]
δ^{15}N range	1.48 [0.28 - 3.23]
SEAc	1.5 [0.04 - 5.39]
SDNND	0.32 [0.01 – 0.93]
Explanatory variable	
Habitat quality (Forest structure)	
Number of vines	4.30 [0.50 – 9.90]
Tree height (m)	8.31 [6.11 – 10.59]
Canopy cover (%)	77.37 [74.20 – 82.90]
Litter volume (m^3)	0.00237 [0.00120 – 0.00441]
Tree basal area (m^2)	0.08 [0.03 – 0.27]
Understory clutter (%)	50.21 [17.17 – 74.17]
Habitat quality (Food resources)	

Arthropod diversity (H´)	1.95 [1.11 – 3.96]
Hemiptera abundance	1.95 [0 – 8]
Isoptera abundance	74.50 [0 – 950]
Coleoptera abundance	41.64 [0 – 186]
Fruit abundance	18.56 [0 – 78.80]
Patch scale	
Core area (m²)	5999.41 [204.11 – 50944.50]
NDVI	0.64 [0.50 – 0.71]
Landscape scale	
Mean patch isolation (MNN) (m)	94.59 [44.14 – 158.38]
Total core area (m²)	987627.3 [78300 – 5888700]
Shape complexity (MPAR)	0.17 [0.06 – 0.43]

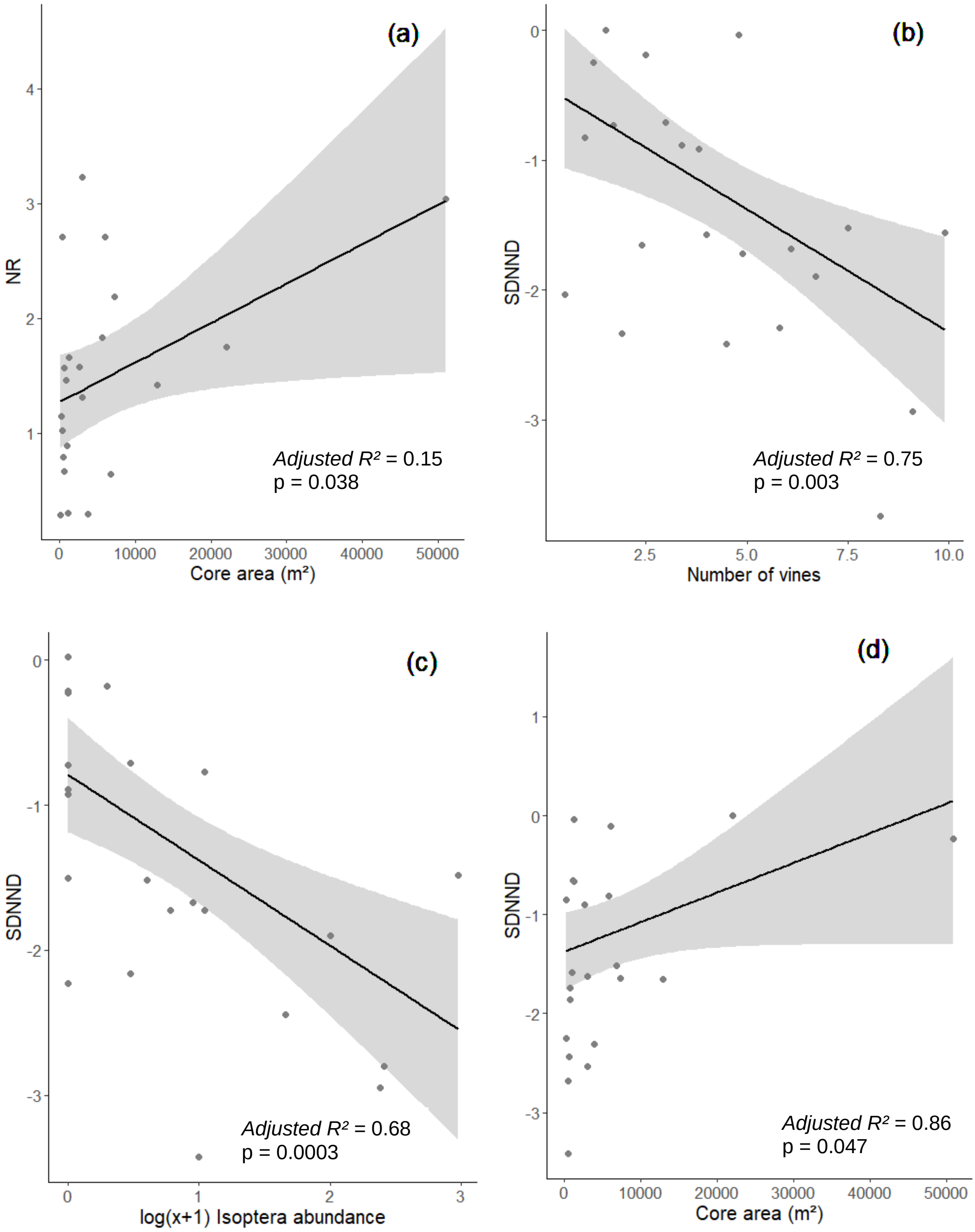

Figure 3. Final regression models revealing the influence of habitat quality (forest structure and food resources), and patch scale predictors on isotopic niche space (Layman et al. 2007a; Jackson et al. 2011) of *Gracilinanus agilis* in the Brazilian Savanna, including: (a) relationship between δ^{15}N range (NR) and patch core area (m²), a patch scale effect; relationships between niche uniformity (SDNND) and (b) mean number of vines -

a forest structure variable; (c) Isoptera abundance - a food resource variable; and, (d) patch core area (m^2).

Discussion

Habitat structure and food resource availability, here treated as measures of habitat quality, as well as spatial scale (patch and landscape) may influence aspects of trophic ecology and network interactions of animal populations (Chapter II, Navarro-López and Fargallo 2015; Camargo et al. 2019; Lei et al. 2019; Muñoz-Lazo et al. 2019). Adopting a multiscale approach to study variations in trophic ecology of animals in altered landscapes should reveal a more complete overview of the ecological mechanisms underlying changes in species responses.

Contrary to our expectations, δ^{13}C range (CR) was not influenced by any predictors within the analyzed scales. Assimilated carbon values were consistent with a major contribution of C_3 resources, corresponding to forest basal resources (Ometto et al. 2002, 2006; Coletta et al. 2009). Cerrado forest plants are predominantly C_3 and do not vary widely in carbon signals (Parron et al. 2004; Coletta et al. 2009), which might result in a small variation in δ^{13}C range of assimilated basal resources of the agile opossum. This result also indicated that the species does not feed on matrix basal resources (C_4 pasture grass), or on matrix invertebrates, revealing high dependency on forest remnants. Furthermore, apparently habitat quality and spatial features do not seem to be important to determine the variation of δ^{13}C range for the studied species.

Contradicting our hypotheses, neither forest structure, food resources, or landscape metrics affected δ^{15}N range. This isotopic niche metric was only influenced at the patch scale, revealing a positive relationship with patch core area, indicating that larger areas with more conserved forests (i.e., weaker edge effects) led populations to feed on a higher diversity of trophic levels. However, NDVI (here used as a patch descriptor of forest density) did not predict variations in δ^{15}N range.

Unfragmented systems and larger patches are expected to harbor higher biodiversity (Fahrig 2003), a context that enables individuals of a population to specialize in different potential food items (in our system, arthropods, fruits, fungi), promoting intraspecific trophic niche variation (Layman et al. 2007b). In fact, fragmentation leads to a reduction in species richness and diversity of arthropods (Kishbaugh and Yocom 2000), also affecting the abundance of trophic guilds, with omnivorous species being more common in forest fragments together with predatory spiders, while herbivores are more abundant in continuous areas and in the forest interior, except for leaf-miner ants, that present higher density in fragments and forest edges (Wirth et al. 2007; Rossetti et al. 2014; Benítez-Malvido et al. 2016). Additionally, forest basal resources (fruits) are also hampered by forest fragmentation (Terborgh 1986, 1992). Thus, since arthropods and fruits are the main food items in the agile opossum´s diet (Camargo et al. 2014), it is expected that they respond to changes in the diversity and availability of these resources, even though we failed to detect a direct effect of food resources on δ^{15}N range. In this sense, our results showing the effects of patch size on δ^{15}N range reveal the potential indirect impacts of fragmentation and other habitat changes cascading through the food web, from changes in resource availability to modification of consumer´s trophic ecology, a pattern that has been detected for terrestrial and aquatic consumers (Chapter II, Layman et al. 2007b; Klarner et al. 2017; Resasco et al. 2018; Muñoz-Lazo et al. 2019).

Moreover, standard ellipse area (SEAc) presented no relationship with the evaluated predictors at any scale. Apparently, the tested variables are not important to determine variations in SEAc. Nevertheless, we were surprised not to find an effect of patch size on this niche metric, since either negative or positive responses to this patch scale predictor are reported elsewhere for different organisms (Chapter II, Layman et al. 2007b; Resasco et al. 2018; Muñoz-Lazo et al. 2019). In Chapter II of this work, we detected an effect of patch size depending on habitat amount in the landscape, but the approach there was related to a broader spatial scale in the response (habitat amount considered was at a scale of 15,000 ha, while here it is of a 1-km radius). These findings highlight that the evaluated scale of response might be important to reveal the effects of habitat modifications on species responses.

Finally, regarding niche uniformity (SDNND), our hypotheses were partially corroborated. This isotopic niche space metric responded to habitat quality (forest structure and food resources), and to patch scale. As expected, concerning forest structure, niche uniformity was negatively related to number of vines. So, in patches with a higher density of lianas, opossum populations presented lower SDNND values, i.e., a similar isotopic trophic niche between individuals. Since increased abundance of vines is a proxy for forest disturbance, mediated by edge effects (Campbell et al. 2018; Laurance et al. 2018), we can infer that perturbed forests lead *G. agilis* individuals to have similar trophic niches. Lianas are an important microhabitat feature selected by *Gracilinanus* (Melo et al. 2013; Camargo et al. 2018), and are also important for insectivorous and omnivorous small mammal species (Hannibal et al. 2020), since these plants promote higher understory connectivity for this small scansorial-arboreal marsupial. Probably a high density of lianas favors individuals to be concentrated in the understory stratum, exploring the available food and shelter resources there located, potentially leading to a higher similarity in trophic niche within the population than would be the case if individuals explored the ground stratum more frequently. This idea is corroborated by Camargo et al. (2019), who found that more structured forests promote higher network nestedness of *G. agilis*, which means that in forests with higher complexity, individuals increase vertical segregation to explore ground and upper strata resources, potentially adding new food items to their diets. So, in a condition of understory microhabitat use preference, enhanced by great availability of lianas, as we found, there would be a potential similarity in trophic niche between individuals. In fact, differences in microhabitat use of vertical strata was found to affect the trophic niche of other mammals species (Hadi et al. 2012; Dammhahn et al. 2013; Reuter et al. 2016).

Moreover, disturbed forests dominated by lianas present changes in tree community composition and dynamics, reduced tree growth and fecundity, elevated tree mortality—specially of late-successional and climax species (Campbell et al. 2015; Laurance et al. 2018)—as well as fragmentation scenarios that can hamper overall resource diversity and availability (such as fruits and arthropod guilds) as a consequence of biodiversity loss (Terborgh 1986; Rossetti et al. 2014; Haddad et al. 2015; Benítez-Malvido et al. 2016). These conditions could also contribute to a higher similarity of trophic niches within populations, even though we failed to detect a direct relationship between SDNND and diversity of food resources (i.e., arthropod diversity).

With respect to food resources, we found a negative effect of Isoptera abundance on SDNND values, revealing that patches with more Isoptera presented higher similarity in trophic niche between opossum individuals within populations. Termites are one of the most abundant insect orders in the Cerrado (Negret and Redford 1982; Pinheiro et al. 2002), representing an important diet item for lizards, anurans, and mammals (Costa et al. 2008; Lessa and Costa 2010; Camargo et al. 2014; Marques-Pinto et al. 2019). Isoptera represents a valuable prey item, because it is a concentrated resource (Abensperg-Traun and Steven 1997) that provides water supply and fat content (DeFoliart 1992; Cooper and Withers 2004). The agile opossum feeds heavily on termites according to their availability in the environment in the wet season, and selects it positively in the dry season, when there are higher energy demands for reproductive activities (Camargo et al. 2014). Given their nutritional importance, and high abundance of these insects in the Cerrado, it is expected that *Gracilinanus* individuals respond uniformly to the availability of this resource, assimilating it in accordance to its abundance, which leads to lower SDNND values (i.e., higher trophic similarity).

Lastly, at the patch scale, SDNND variation was explained by patch core area, revealing that larger patches with more pristine vegetation held opossum individuals with more distinct trophic niche within each population (higher SDNND values). Such patches are expected to have greater biodiversity (Lomolino 2001; Fahrig 2003), potentially offering higher resource diversity and availability (Laurance et al. 2000; Haddad et al. 2015). Moreover, higher patch core area suggests larger amounts of less disturbed habitats within fragments (edge effects), which means that in this condition forest habitat tends to be more structured and complex (Laurance et al. 2000, 2018). Thus, with higher resource diversity/availability, and more opportunities to vertically explore those resources, scansorial-arboreal individuals have more chances to choose between preferred food items, and specialize in different resource types, i.e., resource partitioning (Bolnick et al. 2003; Finke and Snyder 2008), increasing trophic niche differences within the population. In fact, our findings are supported by Camargo et al. (2019), who showed that resource diversity and abundance (e.g., fruits and arthropod diversity) positively affected modularity of *G. agilis* in a Brazilian woodland savanna, indicating that higher resource diversity leads to diet segregation between individuals. Besides, they also found that more structured forests were positively related to nestedness, suggesting that vertical segregation among individuals promote differential resource exploitation between them (Camargo et al. 2019a).

The stable isotopes approach is being continuously adopted to help researchers understand species´ trophic responses to environmental shifts, specially under the present global scenario of landscape change (Chapter II, Layman et al. 2007b; Reuter et al. 2016; Resasco et al. 2018; Magioli et al. 2019; Ribeiro et al. 2019). We have shown that applying “community-wide metrics” of isotopic niche space (i.e., Layman metrics, Layman et al. 2007a) at the population level is a powerful tool to explore changes in the degree of trophic specificity/generality among individuals in a population in human-driven environmental contexts (Bearhop et al. 2004; Layman et al. 2007a, 2012), which helps reveal different aspects of the species trophic ecology.

Furthermore, here we show that analyzing both habitat and broad spatial scales (i.e., patch and landscape) allows us to unveil different ecological mechanisms driving species responses to fragmentation and habitat loss. Under this multiscale approach, this is the first study to evaluate changes in trophic niche space of an organism. In our system, distinct metrics of trophic niche space were related to different patch or/and habitat quality features, but none with landscape scale. These results indicate that smaller scales might be more important to determine changes in trophic niche space of *G. agilis* than the evaluated landscape scale, probably because this small bodied species responds to finer grain environmental changes. In this sense, we suggest that future studies embrace multiscale approaches to advance in the comprehension of the full consequences of landscape change to biodiversity and trophic ecology (Delciellos et al. 2016; Hannibal et al. 2018, 2020); and most of all, we reinforce the need to evaluate the impacts of changes in habitat quality (which is species-specific and requires basic autoecological knowledge of the studied species), usually a neglected aspect of fragmentation effects in ecological research (Mortelliti et al. 2010; Delciellos et al. 2016).

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Appendix I

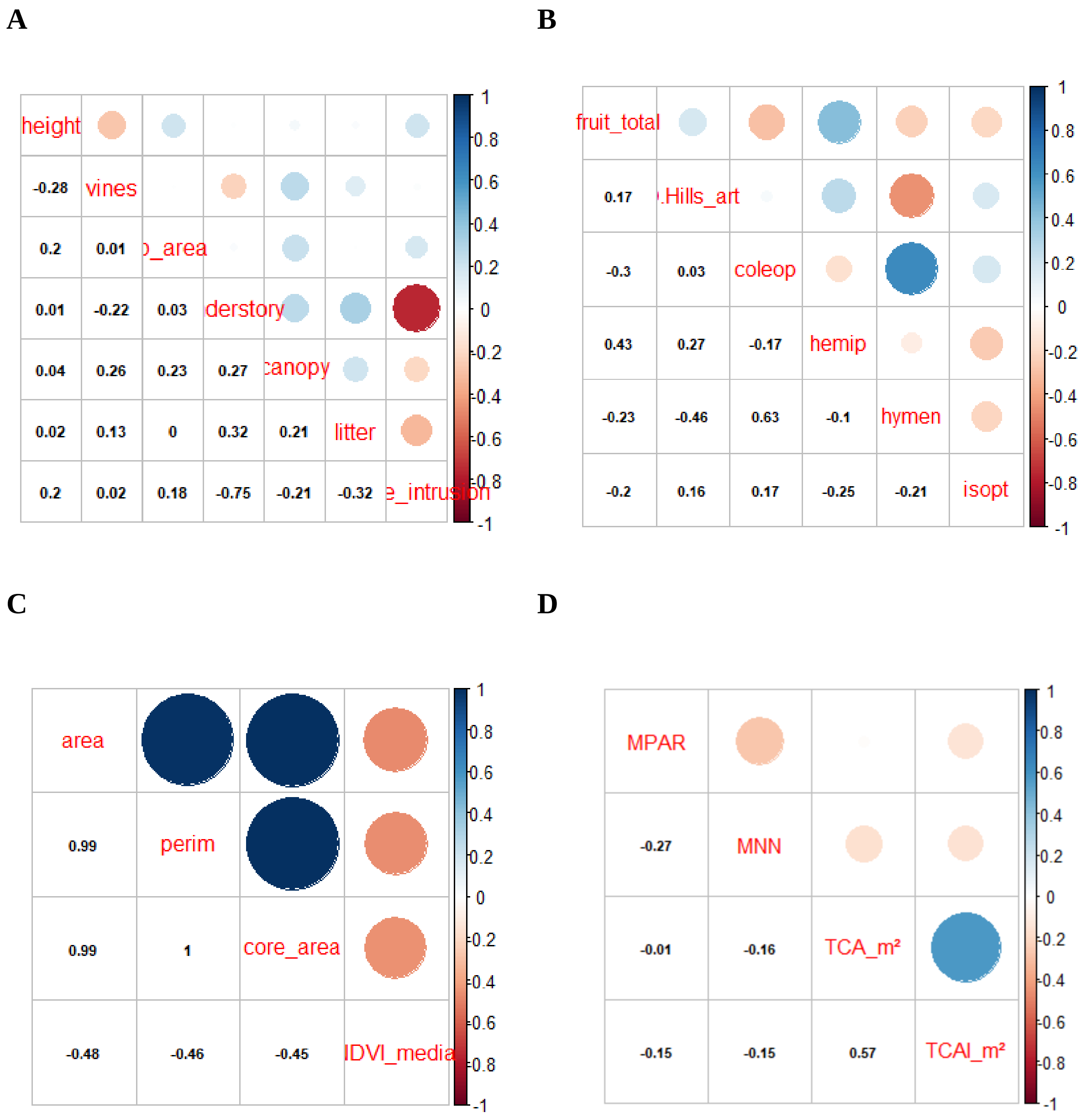

Figure AI. Correlation plots (based on Pearson's correlation coefficients) investigating multicollinearity ($r > 0.5$) in the explanatory variable data set used as predictors of isotopic niche space. Variables are grouped into descriptors of habitat quality [**(A) Forest structure**: Height – Tree height (m); vines – number of vines; b_area – basal area (m^2); understory – understory clutter (%); canopy – canopy cover (%); litter – litter volume (m^3); cattle_intrusion – level of cattle intrusion inside the patch; **(B) Food resources**: fruit_total – total number of fruits; D.Hills_art – Hills Index of arthropod diversity; coleop – Coleoptera abundance; hemip – Hemiptera abundance; hymen – Hymenoptera abundance; isopt – Isoptera abundance], and spatial scales **[(C) Patch:** area – patch area (m^2); perim – patch perimeter (m); core_area – patch area excluding 50 m edges; NDVI_media – normalized difference vegetation index calculated with the mean values in the dry and rainy seasons; and, **(D) Landscape:** MPAR – mean perimeter-area ratio, indicating shape complexity; MNN – mean nearest neighbor distance, indicating mean patch isolation; TCA_m² – total core area (m²) in a 1-km buffer around the focal patch; TCAI_m² - total core area index, proportion of core area in the entire landscape].

Table AI. Final regression models evaluating the influence of habitat quality (forest structure and food resources) and spatial scales (patch and landscape) on the isotopic niche space (Layman metrics) of *Gracilinanus agilis* in the Brazilian Savanna. Response variables: CR – δ^{13}C range; NR – δ^{15}N range; SEAc – standard ellipse area corrected for small sample size; SDNND – standard deviation of the mean nearest neighbor distance. Explanatory variables are grouped into descriptors of habitat quality (forest structure: Height – tree height (m); Vines – mean number of vines; B_area – basal area (m²); Understory – understory clutter (%); Canopy – canopy cover (%); Litter – litter volume (m³); food resources: Fruits – total number of fruits; H´_arth – Shannon Index of arthropod diversity; Coleoptera – Coleoptera abundance; Hemiptera – Hemiptera abundance; Isoptera – Isoptera abundance), and spatial scales (patch: Core area (m²) – patch area excluding 50-m edges; NDVI – normalized difference vegetation index based on mean values in the dry and rainy seasons; and landscape: MPAR – mean perimeter-area ratio, indicating shape complexity; MNN – mean nearest neighbor distance, indicating mean patch isolation; TCA_m² – total core area (m²) in a 1km buffer around focal patch). Significant p-values are indicated in bold. Regression type: glm – Generalized linear model; lm – linear model.

Final model (regression type)	**df**	**Residual Deviance (glm) or F test (lm)**	**p-value (χ^2 or t)**
Habitat scale (forest structure)			
CR ~ 1 (GLM)	21	8.601	0.126
NR ~ 1 (GLM)	21	9.361	0.223
SEAc ~ 1 (GLM)	21	23.668	0.282
SDNND ~ Vines (GLM)	20	14.870	**0.003**
Habitat scale (food resources)			
CR ~ 1 (LM)	21	2.918	0.103

NR ~ 1 (GLM)	21	9.362	0.407
SEAc ~ 1 (GLM)	21	23.668	0.125
SDNND ~ log$_{10}$(x+1) Isoptera (GLM)	20	13.536	**0.0003**
Patch scale			
CR ~ 1 (LM)	21	3.893	0.063
NR ~ Core area (LM)	20	1.441	**0.038**
SEAc ~ 1 (GLM)	21	23.668	8.13 x 10^{-5}
SDNND ~ Core area (GLM)			
Landscape scale			
CR ~ 1 (LM)	21	0.398	0.535
NR ~ 1 (LM)	21	3.563	0.074
SEAc ~ 1 (GLM)	21	23.668	0.496
SDNND ~ 1 (GLM)	21	19.718	0.141

Conclusões

Com o avanço rápido da destruição das florestas neotropicais para conversão em agricultura e pastagem, é de grande importância compreender como as populações e as comunidades animais respondem aos resultantes processos de fragmentação, perda de habitat e degradação dos remanescentes nativos, sob diferentes aspectos. Neste contexto, este trabalho conclui que:

- Os efeitos da configuração da paisagem não foram dependentes da quantidade de habitat disponível na paisagem para determinar as comunidades de pequenos mamíferos.
- De forma geral, o aumento da fragmentação e da perda de habitat levou a um aumento na abundância de pequenos mamíferos.
- Espécies generalistas e especialistas de florestas responderam de formas distintas a esses processos de alteração dos habitats e das paisagens: a riqueza de espécies generalistas foi influenciada positivamente pela quantidade de habitat na paisagem, enquanto o número de espécies especialistas dependeu da qualidade das florestas remanescentes, apresentando uma relação positiva com a cobertura de dossel.
- Os parâmetros da estrutura da paisagem (tamanho de fragmento e proporção de floresta na paisagem) foram mais determinantes para a mudança na composição de espécies do que os parâmetros da qualidade da estrutura remanescentes florestais ao longo do gradiente de fragmentação e perda de habitat.
- As consequências da fragmentação e da perda de habitat vão muito além da perda de espécies, alterando não só os padrões de abundância e composição de espécies, como também a ecologia trófica, amplitude de nicho, estrutura trófica e uso do habitat pelas espécies sobreviventes.
- Nosso estudo contribuiu para mostrar que a fragmentação e perda de habitat podem impactar severamente os papéis ecológicos das espécies. No caso de *G. agilis*, um consumidor onívoro, o avanço da perda de habitat e da fragmentação levou a um aumento da insetivoria em detrimento da frugivoria, prejudicando seu papel como dispersor de frutos e assim, diminuindo potencial de contribuir para a regeneração das florestas remanescentes em paisagens fragmentadas.

- Com relação ao nicho trófico, o efeito da fragmentação foi dependente do contexto de perda de habitat da paisagem, sendo mais intenso em paisagens intermediárias e mais conservadas.
- A espécie modelo não incorporou recursos alimentares presentes na matriz de pastagem, sendo dependente dos recursos presentes nos remanescentes, mesmo em fragmentos bem pequenos e em paisagens mais degradadas. Este dado revela que mesmo fragmentos bem pequenos (menores do que 10 ha) podem ser de grande importância para a sobrevivência das espécies, mesmo para aquelas tolerantes a mudanças ambientais e com alta plasticidade trófica, como é o caso de *G. agilis*.
- Avaliar diferentes aspectos da ecologia trófica de uma espécie e em várias escalas permite maior compreensão da complexidade das respostas ecológicas às alterações ambientais provocadas pela fragmentação e perda de habitat.
- Verificamos que escalas menores (de fragmento e de habitat) se mostraram mais importantes para determinar mudanças no espaço de nicho trófico do marsupial estudado do a escala espacial mais ampla da paisagem.
- A espécie incorporou maior diversidade de níveis tróficos em sua dieta em fragmentos maiores e mais conservados, assim como também apresentou maior dissimilaridade do espaço de nicho nessas áreas. Além disso, indivíduos da mesma população apresentaram nicho trófico mais similar em florestas mais alteradas (indicado pelo maior número de lianas) e quando houve maior abundância de térmitas, um recurso precioso em termos de água e nutrientes.
- Por fim, nossos resultados ressaltam a importância de incluir a avaliação das mudanças na qualidade de habitat dos remanescentes nos estudos de ecologia de paisagem, pois podem ser tão ou mais importantes quanto as escalas espaciais para determinar as repostas das espécies às alterações ambientais resultantes da conversão da vegetação nativa.