MINISTÉRIO DA CIÊNCIA, TECNOLOGIA E INOVAÇÕES
INSTITUTO NACIONAL DE PESQUISAS ESPACIAIS

sid.inpe.br/mtc-m21d/2022/09.07.00.24-TDI

EFFECTS OF THE AGRICULTURAL FRONTIER ADVANCE ON CERRADO BIODIVERSITY: THE RESPONSE OF SMALL MAMMALS TO HABITAT LOSS

Tainá Oliveira Assis

Doctorate Thesis of the Graduate Course in Earth System Science, guided by Dra. Silvana Amaral Kampel, approved in July 14, 2022.

URL of the original document:
<http://urlib.net/8JMKD3MGP3W34T/47JBEPB>

INPE
São José dos Campos
2022

PUBLISHED BY:

Instituto Nacional de Pesquisas Espaciais - INPE
Coordenação de Ensino, Pesquisa e Extensão (COEPE)
Divisão de Biblioteca (DIBIB)
CEP 12.227-010
São José dos Campos - SP - Brasil
Tel.:(012) 3208-6923/7348
E-mail: pubtc@inpe.br

DIGITAL LIBRARY:
Dr. Gerald Jean Francis Banon
Clayton Martins Pereira - Divisão de Biblioteca (DIBIB)
DOCUMENT REVIEW:
Simone Angélica Del Ducca Barbedo - Divisão de Biblioteca (DIBIB)
André Luis Dias Fernandes - Divisão de Biblioteca (DIBIB)
ELECTRONIC EDITING:
Ivone Martins - Divisão de Biblioteca (DIBIB)
André Luis Dias Fernandes - Divisão de Biblioteca (DIBIB)

MINISTÉRIO DA CIÊNCIA, TECNOLOGIA E INOVAÇÕES
INSTITUTO NACIONAL DE PESQUISAS ESPACIAIS

sid.inpe.br/mtc-m21d/2022/09.07.00.24-TDI

EFFECTS OF THE AGRICULTURAL FRONTIER ADVANCE ON CERRADO BIODIVERSITY: THE RESPONSE OF SMALL MAMMALS TO HABITAT LOSS

Tainá Oliveira Assis

Doctorate Thesis of the Graduate Course in Earth System Science, guided by Dra. Silvana Amaral Kampel, approved in July 14, 2022.

URL of the original document:
<http://urlib.net/8JMKD3MGP3W34T/47JBEPB>

INPE
São José dos Campos
2022

Cataloging in Publication Data

Assis, Tainá Oliveira.

As76e Effects of the agricultural frontier advance on Cerrado biodiversity: the response of small mammals to habitat loss / Tainá Oliveira Assis. – São José dos Campos : INPE, 2022.

xxvii + 176 p. ; (sid.inpe.br/mtc-m21d/2022/09.07.00.24-TDI)

Thesis (Doctorate in Earth System Science) – Instituto Nacional de Pesquisas Espaciais, São José dos Campos, 2022.

Guiding : Dra. Silvana Amaral Kampel.

1. Typology. 2. LUCC. 3. Landscape ecology. 4. Scale. 5. Spatial explicit model. I.Title.

CDU 633:581.526

MINISTÉRIO DA
CIÊNCIA, TECNOLOGIA
E INOVAÇÕES

INSTITUTO NACIONAL DE PESQUISAS ESPACIAIS

DEFESA FINAL DE TESE DE TAINÁ OLIVEIRA ASSIS
BANCA Nº096/2022 REG 142476/2017

No dia 14 de julho de 2022, as 14h00min, por teleconferência, o(a) aluno(a) mencionado(a) acima defendeu seu trabalho final (apresentação oral seguida de arguição) perante uma Banca Examinadora, cujos membros estão listados abaixo. O(A) aluno(a) foi APROVADO(A) pela Banca Examinadora, por unanimidade, em cumprimento ao requisito exigido para obtenção do Título de Doutora em Ciência do Sistema Terrestre. O trabalho deve incorporar as correções sugeridas pela Banca Examinadora, a critério e sob revisão final do(s) orientador(es).

Título: "EFFECTS OF THE AGRICULTURE FRONTIER ADVANCE IN THE CERRADO ON BIODIVERSITY: the response of small mammals to land cover changes"

Dra. Maria Isabel Sobral Escada - Presidente - INPE
Dra. Silvana Amaral Kampel - Orientadora – INPE
Dr. Dalton de Morisson Valeriano - Membro Interno – INPE
Dr. Marcelo Passamani - Membro Externo – UFLA
Dr. Eduardo Moraes Arraut – Membro Externo - ITA

---

sei! assinatura eletrônica

Documento assinado eletronicamente por **Silvana Amaral Kampel**, **Pesquisadora**, em 19/07/2022, às 10:50 (horário oficial de Brasília), com fundamento no § 3º do art. 4º do Decreto nº 10.543, de 13 de novembro de 2020.

---

sei! assinatura eletrônica

Documento assinado eletronicamente por **Marcelo Passamani (E)**, **Usuário Externo**, em 20/07/2022, às 11:05 (horário oficial de Brasília), com fundamento no § 3º do art. 4º do Decreto nº 10.543, de 13 de novembro de 2020.

---

sei! assinatura eletrônica

Documento assinado eletronicamente por **Maria Isabel Sobral Escada**, **Tecnologista**, em 22/07/2022, às 14:05 (horário oficial de Brasília), com fundamento no § 3º do art. 4º do Decreto nº 10.543, de 13 de novembro de 2020.

---

sei! assinatura eletrônica

Documento assinado eletronicamente por **Eduardo Moraes arraut (E)**, **Usuário Externo**, em 22/07/2022, às 18:18 (horário oficial de Brasília), com fundamento no § 3º do art. 4º do Decreto nº 10.543, de 13 de novembro de 2020.

---

sei! assinatura eletrônica

Documento assinado eletronicamente por **Dalton de Morisson Valériano**, **Pesquisador**, em 21/09/2022, às 10:09 (horário oficial de Brasília), com fundamento no § 3º do art. 4º do Decreto nº 10.543, de 13 de novembro de 2020.

Referência: Processo nº 01340.002970/2022-75 SEI nº 9720059

“The question is whether any civilization can wage relentless war on life without destroying itself, and without losing the right to be called civilized.”

Rachel Carson

To my Family and my friends that were with me in this journey.

ACKNOWLEDGEMENTS

I am grateful to my supervisor, Dr. Silvana Amaral, for believing in my work and for all the support in this thesis development, for the knowledge she shared, for the long talk about my frustrations, and for insights to find solutions. I am deeply honored to learn with her. I am also grateful for all the emotional support during this period.

I am also grateful to my supervisor during the period at Carleton University, Dr. Lenore Fahrig, for receiving me at her laboratory GLEL, for discussing my questions in this thesis, helping me to design the papers, and for reviewing it.

I am thankful to Fundação de Amparo à Pesquisa do Estado de S. Paulo – FAPESP to supporting the project (2017/20011-8). We also acknowlege the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Finance Code 001 for the scholorship. I am also thankful to Dr. Marcelo Passamani, Dr. Nilton Cáceres, Dr. Marcus Vinícius Vieira, Dr. André Mendonça, Dr. Emmerson Vieira, and Dr. Natália Leiner for giving me the data necessary to write this thesis.

I am thankful to Dr. Eduardo Arraut and Dr. Pedro Andrade for discussing the ABM with me, helping me with the references in this type of study and helping me to design my theoretical model, and helping me to design the model in TerraME.

I am also grateful for all the support I had from the CCST, to the workers who support the students specially Ângela and Mariana, and the coordinators Dr. Kleber Naccarato and Dr. Laura Borma.

I am grateful to LISS for all the knowledge and joy we shared. I am especially grateful to Danielle, Danilo, Bruno, Gisele, Anielli e Renata who helped me to type while I was hilling. I will always remember and be grateful for this gesture of empathy.

I am grateful to the friends I have made during and because of the undergraduate program in Earth System Science, the colleagues from 2017, particularly, Mariane Reis, and my friends Olivier Heldwein, and Ishdeep Sign. Thank you for bringing so much joy to my days and making this period easier.

I am grateful to my supervisors at work, especially Samuel Campos and Mauro Leite, who gave me more time to dedicate to my thesis. Also, I want to thank Naiara Santos, Nilton Lima, and Dr. Thales Korting for lending me their computer to run my model.

I am thankful for those who are by my side in every step of my life, my family. I am grateful to my parents, Horacio and Maria Tereza, for giving more than necessary for a good life and being the example, I want to follow in my life. My sister Talita and my brother-in-law Gav, for supporting me in all the decisions I make and for bringing to this world the one that is all my joy, Matias.

Finally, I am thankful to the best husband I could have, Marcos, for being by my side, supporting my decisions, and taking the risk with me. He is my reviewer, my emotional support, my best friend, and my love.

ABSTRACT

The agricultural frontier is considered one of the main drivers of deforestation in the last century. Beyond several environmental consequences, the loss of natural habitats due to deforestation directly affects biodiversity. Inserted in this context, the Brazilian Cerrado has been losing native vegetation since the colonial period, and its area had already been reduced to nearly 50% of its original extent by 2013. This study aims to understand the effects of the land cover changes on the fauna of small mammals in the Brazilian Cerrado. To accomplish this main objective, it was necessary to understand: (i) the effects of agriculture type and conservation policies on the loss and fragmentation of natural habitats in the Brazilian Cerrado; (ii) how the process of expansion over natural habitats occurs throughout time; (iii) how to define scale and representation of landscapes in mammal studies; (iv) the role played by the anthropogenic matrix to improve the landscape quality; and (v) if the landscape changes differently affect small mammals' communities in different Cerrado types – forest, savanna, and grasslands, by modeling the interaction between small mammals and the Cerrado landscape. This thesis advances in the understanding of the impact of the anthropogenic land cover on the patterns of natural habitats in the Cerrado landscape considering both: habitat loss and fragmentation. Based on the results, the main implications of this thesis are: (a) the need to preserve the few contiguous fragments of this biome that have the function of preserving its natural processes; (b) the development of polices to protect the Cerrado natural habitats for croplands and pasturelands; (c) the necessity to keep the Legal Reserve in the Brazilian Forest Code because most of the currently natural habitat in under its protection; (c) to consider the best scale to analyze the effects of landscape, it is necessary to observe the elements of the landscape that affect biological responses; (d) to represent the components of the landscape the biological processes should be used as a guide to define spatial scale and representation; (e) the importance of considering the matrix type to design a more conservation- friendly landscape, not only to increase permeability but to consider the impacts of the matrix type on natural communities' composition; (f) the Agent-based Model (ABM) approach brings the possibility to understand long term interactions between small mammals populations and the landscape changes.

Keywords: Typology. LUCC. Landscape Ecology. Scale. Matrix. Spatial Explicit Model.

EFEITOS DO AVANÇO DA FRONTEIRA AGRÍCOLA NA BIODIVERSIDADE DO CERRADO: A RESPOSTA DOS PEQUENOS MAMÍFEROS À PERDA DE HABITAT

RESUMO

A fronteira agrícola é considerada um dos principais causadores do desmatamento no último século. Além das diversas consequências ambientais, a perda de habitat naturais afeta diretamente a biodiversidade. Inserido neste contexto, o Cerrado brasileiro tem perdido suas áreas desde o período colonial, e a área atual já foi reduzida a menos de 50% de sua extensão original. Este estudo tem como objetivo entender os efeitos das mudanças de uso e cobertura do solo na fauna de pequenos mamíferos do Cerrado brasileiro. Para atingir este objetivo foi necessário entender (i) os efeitos do tipo de agricultura e das políticas de conservação da perda e fragmentação de habitats naturais do Cerrado; (ii) como o processo de expansão sobre áreas naturais ocorreu ao longo do tempo;

(iii) como definir escala e representação de paisagem em estudos de pequenos mamíferos; (iv) o papel das matrizes antropogênicas em melhorar a qualidade da paisagem para pequenos mamíferos e, (v) se as mudanças na paisagem têm efeitos diferentes na população de pequenos mamíferos dentro de floresta, savana ou campo, modelando as interações entre pequenos mamíferos e paisagem do Cerrado. Esta tese avança no entendimento do impacto das coberturas antropogênicas nos padrões de habitat natural, considerando perda e fragmentação de hábitat. Baseado nos resultados, as principais implicações desta tese são: (a) a necessidade de preservar as poucas manchas contínuas no bioma que possuem função de manter os processos naturais; (b) o desenvolvimento de políticas de proteção distintas para áreas agrícolas e de pastagem; (c) a necessidade de se manter as Reservas Legais no Código Florestal Brasileiro, uma vez que a maior parte dos habitats naturais do Cerrado se encontram dentro destas; (d) para considerar a melhor escala para análises da paisagem é necessário observar os elementos da paisagem que afetam os processos biológicos; (e) representar os componentes da paisagem para os processos biológicos deve ser guia para definição de escala e representação da paisagem; (f) a importância de se considerar o tipo de matriz ao delinear uma paisagem mais amigável à biodiversidade não deve considerar apenas o aumento da permeabilidade, mas os impactos causados na composição de comunidades biológicas; (f) a abordagem de Modelagem Baseada em Agente (ABM) traz a possibilidade de entender as interações em longo prazo das populações de pequenos mamíferos e mudanças na paisagem.

Palavras-chaves: Tipologia. Mudanças De Uso e Cobertura Do Solo. Ecologia da Paisagem. Escala. Matriz. Modelo Espacialmente Explícito.

LISTA DE FIGURAS

LISTA DE TABELAS

LISTA DE SIGLAS E ABREVIATURAS

ABM	Agent-Based Model
DistLM	Distance-based multivariate multiple regression
GLM	General Linear Model
INPE	Instituto Nacional de Pesquisas Espaciais
UFLA	Universidade Federal de Lavras
UFRJ	Universidade Federal do Rio de Janeiro
UFSM	Universidade Federal de Santa Maria
UFU	Universidade Federal de Uberlândia
UnB	Universidade de Brasília
SMAC	Small mammals at the Cerrado Changes

SUMÁRIO

Pág.

1 INTRODUCTION

The expansion of agriculture is considered one of the main drivers of deforestation in the last century (LAURANCE; SAYER; CASSMAN, 2014). Beyond several environmental consequences, the loss of natural habitats due to deforestation directly affects biodiversity (MYERS et al., 2000a). Inserted in this context, the Brazilian Cerrado has been losing native vegetation since the colonial period, and its area had already been reduced to nearly 50% of its original extent by 2021 (MAPBIOMAS v.7, 2022).

There were distinct phases of land cover changes due to anthropogenic causes across the Cerrado Biome. At first, the Cerrado biome was occupied by a sparsely distributed population with the practice of subsistence agriculture. Then, the intensification in the use of this biome started with charcoal production. The use of forage grasses well adapted to acid soils, mainly the grasses of African origin such as the *Urochloa* spp., made possible the extensive production in this biome in the 1960s. The expansion of the planted pasture together with the construction of the Brazilian Capital, Brasília, were a new phase of the Cerrado occupation. The expansion of the road network in the Center-West Region of Brazil between the 1950s and 1960s enabled access to the Cerrado areas (RATTER; RIBEIRO; BRIDGEWATER, 1997a). Then, after the 1970s the techniques of genetic improvement, soil correction, and agricultural mechanization started a new phase of expansion over the Cerrado areas. The Cerrado soil, previously considered inadequate for cultivation, becomes fertile, and together with the flat relief favored the establishment of the agricultural frontier (CARVALHO; DE MARCO; FERREIRA, 2009a; MARTINELLI et al., 2010).

These technologies favored agriculture activities mainly linked to grain cultivation, especially soy, which expands the most in this biome (PHALAN et al., 2013). The threats suffered by the Cerrado because of intense land cover changes, added to the fact that it is a biome with many endemism and great biodiversity, characterizes it as a hotspot, a priority area for world conservation (MYERS et al., 2000a).

To understand how biodiversity responds to habitat loss and persists in human-dominated environments, the first studies considered the landscape as a binary environment: native patches within an anthropogenic matrix, e.g., the traditional approach of the Biogeography of the Islands (HENGEVELD, 2002). This approach helped to understand the role of patch size and isolation in maintaining biodiversity in a fragmented landscape. However, the anthropic matrix is not impermeable to species as it has been considered, but rather it allows different degrees of percolation according to its structure, and it can also serve as a habitat for some species (PREVEDELLO; VIEIRA, 2010b). Thus, the survival of species in a human-dominated landscape depends on their ability to perceive the environment, occupy space, and move in an altered landscape (GASCON et al., 1999).

Small mammals, a group formed by small rodents and marsupials, have a special function within the dynamics of human-dominated landscapes because the group comprises species that are prey, mesopredators, seed dispersers, and seed predators (CAMARGO et al., 2011). Because of this, the dynamics of this group in fragmented environments are key to the maintenance of ecological functions. In addition, small mammal species can act as vectors of diseases such as hantavirus (VIEIRA et al., 2009). Thus, it is necessary to understand the mechanisms of relationships between species, habitat, and natural and anthropogenic land covers.

Relating species dynamics to landscape dynamics is a challenge since this process results from the interactions between species and the environment. A methodological alternative to studying these systems and their interactions is through computational modeling, which provides tools to represent the processes and simulate different scenarios. Among the computational modeling methods, the agent-based model (ABM) brings the perspective of the behavior of agents, allowing the observation of interactions between them and the patterns that emerge from these interactions (GILBERT, 2008). In this approach, the agent can be represented, for example, by animal groups or individuals, organizations, and the environment (PARKER et al., 2003). A spatially explicit agent-based model is an adequate tool for understanding the dynamics of species over time and space. It allows us to observe the consequences of factors linked to the behavior of species for the maintenance of these species in the environment, which in turn also changes over time.

Using agent-based models to represent the interactions between species and environments is a helpful tool to understand biological responses in landscape ecology (WILENSKY; RAND, 2015). The application of this type of modeling to simulate the small mammal's behavior helps to understand dispersion patterns, the mortality in anthropogenic-matrix, and the conservation value of landscape structures such as corridors or steppingstones (MARTIN; FAHRIG, 2016; ROCHA et al., 2021). However, reducing the uncertainty in the modeling process requires using as input the most accurate data available (WILENSKY; RAND, 2015).

Building good models in landscape ecology requires understanding landscape changes and how species relate to landscape structures. However, to be able to build good models it is necessary to achieve a good parametrization and to have enough knowledge about the process to be simulated. In order words, previous studies are essential to support the decisions to be taken in the model. Because of this, the structure of this thesis was formulated to acquire knowledge about the Cerrado landscape and the policies that lead to land use and land cover changes at first. This part was crucial for the understanding of the spatial component of our model. Then, we discussed the adequate scale to landscape ecological studies on mammals and proposed directions to follow in the scale’s choices. Obtaining the adequate scale we could evaluate how the small mammals' community answers to different contexts of habitat loss and matrix predominance in the Cerrado context. Finally, after obtaining the knowledge of our spatial parameters, the adequate scale, and how the biological agents perceive the landscape, we designed an agent-based model to understand how the small mammals answer to land cover changes throughout time.

Having presented the general context, this study aims to understand the effects of the land cover changes on the fauna of small mammals in the Brazilian Cerrado. To accomplish this main objective, it was necessary to understand: (i) the effects of agriculture type and conservation policies on the loss and fragmentation of natural habitats in the Brazilian Cerrado; (ii) how the process of expansion over natural habitats occurs throughout time; (iii) how to define scale and representation of landscapes in mammal studies; (iv) the role played by the anthropogenic matrix to improve the landscape quality; and (v) if the landscape changes differently affect small mammals' communities in different Cerrado types – forest, savanna, and grasslands, by modeling the interaction between small mammals and the Cerrado landscape. Each topic was discussed in an individual study, reported as a scientific article, considering their specific questions, hypothesis, and methodology based on geographical data and fieldwork data for Cerrado small mammal species.

This thesis advances in the understanding of the impact of the anthropogenic land cover on the patterns of natural habitats in the Cerrado landscape considering both: habitat loss and fragmentation. Then, with the understanding of the impact on the Cerrado landscape, we evaluated the role played by the conservation policies to protect natural habitats in Cerrado. After knowing the landscape patterns, we advanced in the discussion on the best practices in defining scale in landscape ecology studies, specifically for small mammals, the group used in this study. After this, we explored for the first time, how the small mammals' community from different habitat types answers to different anthropogenic land cover. And finally, we bring as a novelty the agent-based model to discuss the time response of population natural from different habitat types – forest, savanna, and grassland - to land cover changes.

After this general introduction, the second chapter presents the theoretical basis for this thesis, followed by five papers that seek to answer the questions about the Cerrado land use and cover changes and their relationship with the small mammal community. The final chapter presents the discussion and conclusion, pointing to the main implications of this thesis.

2 THEORETICAL BACKGROUND

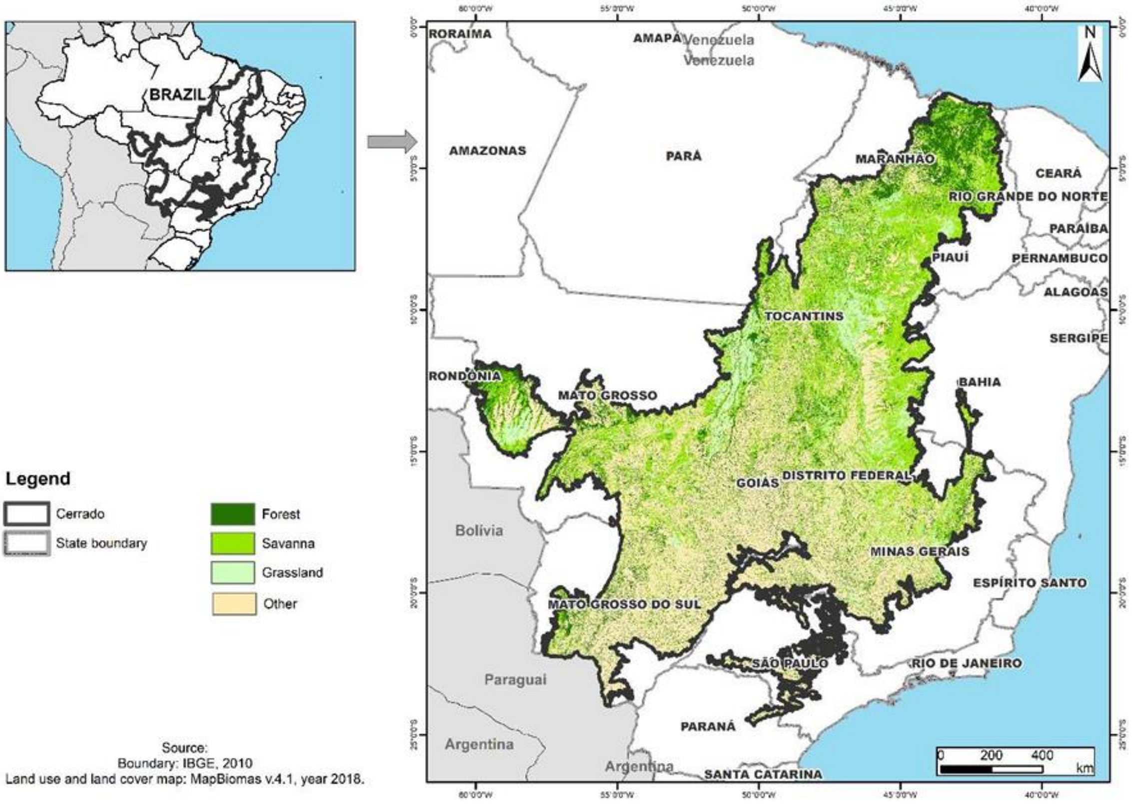
This chapter presents the general theoretical basis that supported the scientific questions proposed in this thesis. It begins by introducing the Cerrado biome and the current changes in its land cover. Next, it explains how habitat loss occurs and how this process can affect the small mammal community. To approach this theme, it explores the landscape ecology concepts in the study of small mammals, bringing to it the concepts of changes, structures, and flows that occur in the landscape. Finally, it presents agent-based models as a potential tool to better understand the relationships between species' persistence in human-altered landscapes.

2.1 The Cerrado

2.1.1 General description

The Cerrado, or the Brazilian Savanna, is a biome located in central Brazil, with most of the area in the Central-West Region, but it also occupies part of the Southeast, North, and Northeast Regions. It covers around 23%, approximately 2 million km^2, of the Brazilian territory, distributed in 11 Brazilian states and the Federal District (Figure 2.1). There are approximately 25 million inhabitants in the Cerrado biome (IBGE, 2010). It has a seasonal tropical climate, with a dry winter. The annual average temperature ranges from 22ºC to 23ºC and the average annual precipitation from 1,200 mm to 1,800 mm (RATTER; RIBEIRO; BRIDGEWATER, 1997a).

Figure 2.1. The Cerrado biome limits and its three main vegetation types: forest, savanna, and grassland.



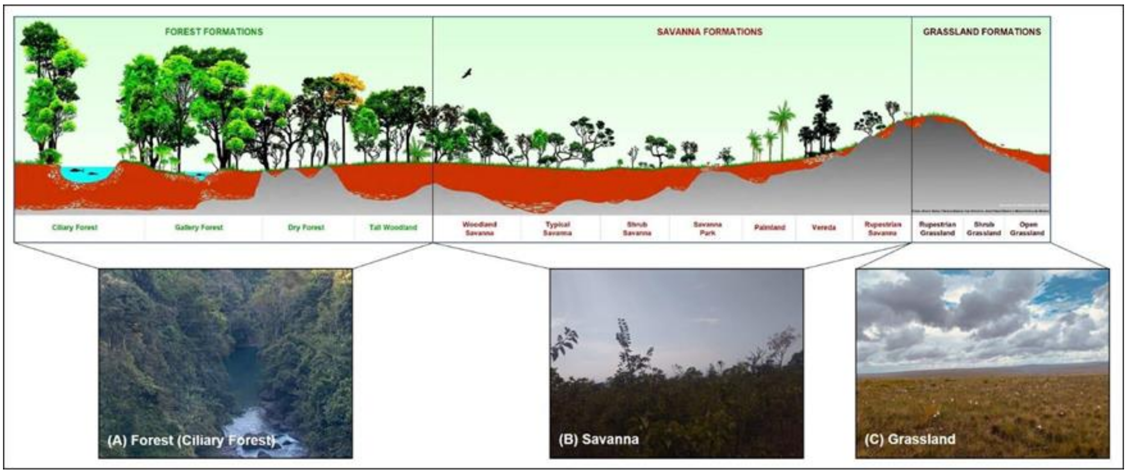
Source: The author.

The Cerrado soil is predominantly acid and dystrophic (REATTO; CORREIA; SPERA, 1998). Also, the soils usually have calcium and magnesium, and high aluminum content (FURLEY; RATTER, 1988). The Oxisols are dominant in the Cerrado biome (FURLEY; RATTER, 1988). Usually, the soils are well-drained with portions of water retention in the surface horizons related to the clay and organic carbon contents (GOMES et al., 2004).

The Cerrado has vegetational formations that vary from grass predominance to forest formations with 5 to 8m trees (RATTER; RIBEIRO; BRIDGEWATER, 1997b). Within the Cerrado biogeographical domain, there are unique formations that depend on altitude and soil type (RIBEIRO; FREITAS, 2010a). This diversity in its formations makes it a megadiverse biome (MYERS et al., 2000b). This can be evidenced, for example, by the plant diversity that can vary from 10 to 120 species per hectare (RATTER; RIBEIRO; BRIDGEWATER, 1997b).

Usually, the Cerrado formation is composed of two layers, a wood layer with trees and large shrubs and a ground layer with small shrubs and herbs. Also, the vegetation has features that make it resistant to fire, such as thick and very lignified bark, thick cuticles, sunken stomata, and lignified leaves. Additionally, this biome includes different phytophysiognomies from grasslands to forests (Figure 2.2). The grassland can vary from open fields to grassland with scattered trees. The savanna has herbaceous vegetation with around 30% of trees and shrubs with a small part of a crown. Finally, the “cerradão” and the stream forests, hereafter called forests, have a canopy formation with trees and shrubs. Savanna and grasslands usually occur on strongly drained soil with a deep water table and seasonal water deficit at the topsoil level. While grasslands occur with low soil fertility, typical savanna can occur with high soil fertility in terms of base saturation. Forests occur on high moisture soil (“cerradão”) or permanently waterlogged or riversides (stream forest) (BOTREL et al., 2002).

Figure 2.2. Cerrado phytophysiognomies formations.



Forest (stream forest (A)) has canopy formation with trees and shrubs, savanna (B) has a mix of an herbaceous layer with trees and shrubs, and grassland (C) is an open field where scattered shrubs may occur.
Source: Adapted from Ribeiro e Walter (2008).

During the dry season, leaf loss by vegetation is common, causing an accumulation of dry biomass on the soil. This accumulation of biomass favors the occurrence and the spread of fire, an agent that is part of the natural dynamics of this biome (Klein et al., 2002). Despite the challenges in monitoring the fire in the Cerrado (NOGUEIRA et al., 2017a, 2017b), the interval between fires is well known. In general, the fire interval varies from 3 to 6 years and the savanna is the Cerrado type with the shortest interval and the forest the longest one (ALFREDO C. PEREIRA JUNIOR, SOFIA L. J. OLIVEIRA, JOSEM. C. PEREIRA, 2014). However, the time plant populations take to recover from fire damage depends on the species' geographic distribution and adaptations (DE ARRUDA et al., 2018).

2.1.2 Land cover changes in the Cerrado

Brazil is among the five tropical countries with the greatest expansion of the agricultural frontier over native areas, together with Nigeria, Indonesia, Ethiopia, and Sudan (DOBROVOLSKI et al., 2011; PHALAN et al., 2013). After the Amazon biome, the Cerrado is the second biome with the largest area in Brazil (RATTER; RIBEIRO; BRIDGEWATER, 1997b) and it has been suffering impacts from human activities since the colonial period. In Brazil, between 1985 and 2017, the farming, crops plus pasture, expanded at a rate of 1.7% per year, and in the Cerrado, 0.9% per year. On the other hand, both forest and grassland had an annual reduction rate of 0.34% in Brazil, but in the Cerrado, the forest had a faster reduction rate (0.6% per year) than grassland (0.2% per year) (SOUZA et al., 2020).

The expansion of human activities over native areas of the Cerrado biome in recent decades calls attention because it increases the loss of native species (SECRETARIAT, 2019). Despite being megadiverse, the Cerrado has 307 species on the list of endangered species. Among the 4,800 estimated endemic species for the biome, 123 are on the endangered species list (BRASIL, 2014). Furthermore, the high regional diversity resulting from its different formations means that conservation strategies for this biome should not be spatially concentrated, making it difficult to choose priority areas (RATTER; RIBEIRO; BRIDGEWATER, 1997b). According to a 2,008 analysis, only 6.5% of Cerrado's native areas are protected by Conservation Units (FRANÇOSO et al., 2015).

The New Forest Code (Law No. 12,651 of 2012) has a special impact on this scenario, mainly because 53% of Brazilian native vegetation is found within private properties (SOARES-FILHO et al., 2014; STRASSBURG et al., 2017). In this context, the Cerrado is the biome with the greatest potential area for the expansion of agribusiness in a legal manner, 40% of its current native area being legally able to be converted. The impacts caused by the New Forest Code can be especially relevant to Cerrado vegetation types that occur in restricted areas such as rupestrian fields and altitude fields (RIBEIRO; FREITAS, 2010b). The persistence of the scenario with a low number of areas destined for conservation, as well as the agricultural expansion, motivated by land price speculation and the encouragement of agribusiness as an economic model, would lead to a reduction in the number of native remnants and a decrease in connectivity in the landscape, estimating a loss of approximately 30% of native Cerrado areas by 2050 (STRASSBURG et al., 2017).

Maintaining the landscape with a greater number of remnants and high connectivity is essential for maintaining biodiversity as it allows for reproduction and foraging (BARRETO et al., 2012). A high number of connected remnants would increase the habitat area, favor dispersal movement, and enhance gene flow (FORMAN, 1995). Besides, the native cover increases the environmental services such as maintaining soil moisture and carbon cycling (BATLLE-BAYER; BATJES; BINDRABAN, 2010; STAN et al., 2015). Understanding the consequences of the process of land cover changes on the biodiversity of the Cerrado is essential to support decisions about the conservation of this biome.

2.2 The study of Cerrado and small mammals through landscape analysis

Cerrado mammals have been impacted by habitat loss, with 12% of threatened mammal species in the Cerrado biome (COSTA et al., 2005). Small mammals account for 85% of mammal species in the Cerrado and are the most affected by the habitat loss of this biome (CÁCERES et al., 2010a). The high diversity of small mammals is justified by the heterogeneity of plant formations, in addition to climatic factors and differences in humidity (BONVICINO; LEMOS; WEKSLER, 2005; DINIZ-FILHO et al., 2008). The open formations have a composition of small mammals more similar to each other, while gallery forests and forest formations present differences in the Cerrado fauna composition (ALHO; PEREIRA; PAULA, 1986) and can serve as a refuge in times of drought and the presence of fire (CARMIGNOTTO; BEZERRA; RODRIGUES, 2014; RAMOS PEREIRA et al., 2013).

There is a consensus that the way small mammals perceive the environment is crucial to understanding the mechanism of their persistence in the landscape (HONORATO et al., 2015; PREVEDELLO; VIEIRA, 2010b). Thus, movement and perceptual capacity depend on the configuration of the landscape (ZOLLNER; LIMA, 1997). The use of space affects the response of species to a human-dominated landscape (JACKSON; FAHRIG, 2012; MELO et al., 2017a).

For a study in landscape ecology, three components must be addressed: structures, dynamics, and flows (FORMAN, 1995). Here we are going to discuss structures, dynamics, and flows addressed to small mammals in the Cerrado. As the Cerrado landscape is human-dominated, it has three types of structure: i) patches of native vegetation, ii) corridor, usually a linear shape of native vegetation, and iii) matrix, an anthropogenic cover, considering the majority area of the Cerrado biome. Dynamics occur over time, and in this study, among the processes that occur in the Cerrado, we restricted the scope to habitat loss. Flows are related to the transfer of matter, energy, or biotic material. Thus, the effect of fire on the small mammal community will be discussed as abiotic fluxes, and the behavioral aspects of species and how they see landscape structures as biological fluxes. More details on structures, dynamics, and flows will be presented in the following topics (2.2.1, 2.2.2, and 2.2.3).

2.2.1 Landscape structures

According to Forman (1995), a landscape mosaic is composed of three elements that can have a natural or anthropogenic origin, namely: patch, corridor, and matrix. Each of these landscape elements can be measured according to their characteristics that are related to the processes that occur within this landscape. Thus, a patch can be measured by size, shape, or neighborhood; a corridor can be measured for its width, connection, and linearity; and a matrix can be measured for its length, continuity, and heterogeneity. These environments are separated by their borders.

A patch is a non-linear area unit, relatively homogeneous (there may be microheterogeneity in its interior), and which differs from its surroundings. Thus, patches can have different sizes, shapes, and degrees of isolation (FORMAN, 1995). For small mammals from Cerrado, the percentage of native cover in the landscape has a greater influence on the community than the size of the patch or the isolation between them (MELO et al., 2017a). This positive response to the increase of native cover is common in biodiversity and is justified by the fact that it usually means an increase in the natural habitat of species (FAHRIG, 2017). But, although there is a greater relationship with the landscape, the species present within the small patches and in patches' edges can, in some areas, be a subset of the community present in the large fragments. This subset is usually dominated by generalist species in terms of habitat (CÁCERES et al., 2010a).

A similar pattern of richness, defined as the number of species, to that found in small fragments can also be found in corridors of native vegetation (FIALHO; CERBONCINI; PASSAMANI, 2017). Corridors are narrow strips of vegetation characterized by having an edge gradient in which their sides border adjacent ecosystems different from their composition (FORMAN, 1995). In landscape ecology, the corridor plays an important role in connecting the mosaic and can also act as a form of habitat (FIALHO; CERBONCINI; PASSAMANI, 2017; PARDINI et al., 2005). For small mammals, the effect of corridors has been more studied for Atlantic Forest and transition regions between Atlantic Forest and Cerrado, both with forest formation. These studies show that in landscapes where the native area cover is reduced, the corridors can have a habitat function, mainly for generalist species and edge specialists (FIALHO; CERBONCINI; PASSAMANI, 2017) and conductors that facilitate the flow of individuals (ROCHA; PASSAMANI; LOUZADA, 2011).

The last landscape structure addressed is the matrix, a structure that can offer greater or lesser disturbance to native species. Matrix is the predominant cover of the landscape (FORMAN, 1995). Because the matrix is the largest area within the landscape, it is responsible for controlling the dynamics within it. This means that when introducing a matrix of anthropic origin, it may have different levels of permeability for native species (DRISCOLL et al., 2013).

A matrix can be measured in its complexity, which considers vertical stratification, and in its heterogeneity, measured horizontally in the landscape (AUGUST, 1983). Vertical stratification considers the formation of strata in the vegetation, such as undergrowth, understory, and canopy. The structure of the matrix (in this study understood as vertical stratification and heterogeneity) and the type of management play a crucial role in the maintenance of species within the remnants and define the quality of the matrix (BRADY et al., 2011; FISCHER; THIES; TSCHARNTKE, 2011). This fact is due to the perception that species have of the environment, defined as perceptual capacity (ZOLLNER, 2000), and the tendency to avoid the risk of predation and to remain within the patch (ZOLLNER; LIMA, 2005). Also, the quality of the matrix can modulate the threshold of native vegetation to species extinction (ARROYO-RODRÍGUEZ et al., 2020; OLIFIERS; GENTILE; FISZON, 2005). A better matrix can improve the quality of the landscape such that the native vegetation threshold of habitat amount for species maintenance can be smaller (BOESING; NICHOLS; METZGER, 2018).

In the study of small mammals, connectivity through the matrix was initially attributed only to generalist species in terms of habitat (OLIFIERS; GENTILE;

FISZON, 2005). However, with the advancement of studies focused on the matrix, it was found that, although generalists can inhabit the matrix and have a greater ability to cross it (PÜTTKER et al., 2013, p. 2013), specialists can move through a more complex matrix, more permeable to the movement (PREVEDELLO; VIEIRA, 2010b). However, the understanding of the effects of the matrix on small mammals considering the particularities of the Cerrado is still poorly understood.

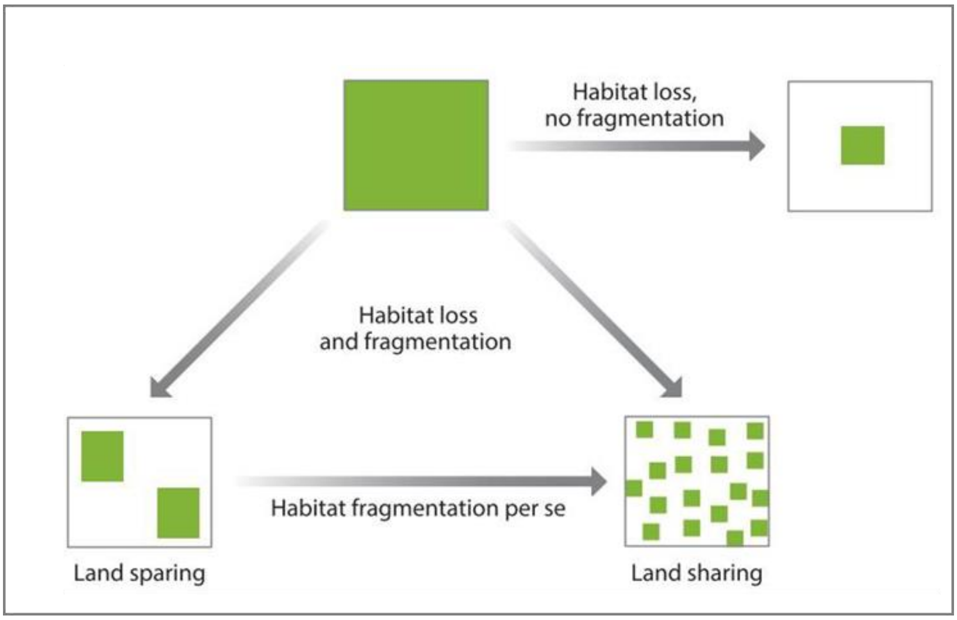
2.2.2 Habitat loss

Among the processes of change that occur in a landscape that involve natural and anthropogenic changes (FORMAN, 1995), habitat loss has the greatest impact on biodiversity (MYERS et al., 2000a). Due to this fact, it is central to describe the habitat loss in the landscape and the changes it causes in the landscape patterns.

2.2.2.1 Land sparing, land sharing, and fragmentation per se

The process of habitat loss can result in one smaller patch than the original one in a matrix of the anthropogenic origin or divide habitat areas into smaller portions, causing landscape discontinuity, and increasing patch isolation (FORMAN, 1995). In this process, previously contiguous natural areas result in a heterogeneous landscape, with patches of native vegetation and human-altered cover environments (METZGER, 2009). The process of habitat loss (Figure 2.3) can result in a more fragmented landscape with a greater number of patches, smaller, and less isolated (land sharing); or in a less fragmented landscape with the natural vegetation concentrated in a smaller number of patches, bigger, and more isolated (land sparing); or also in no fragmentation, but decreasing the patch area (FAHRIG, 2003). Considering this, land sharing is a process of habitat loss resulting in a lot of small patches, with more connectivity, and smaller patches, being a more fragmented landscape. And land sparing results in a less connected landscape with bigger patches, or a less fragmented landscape (FAHRIG, 2003). A process of habitat loss that results in landscapes with the same amount of habitat, but differs in the amount and size of patches is **fragmentation per se** (FAHRIG, 2017).

Figure 2.3. Habitat loss results in no fragmentation, a less fragmented landscape (land sparing), or a high fragmented landscape (land sharing).



Source: Fahrig (2017).

2.2.2.2 The study of fragmentation

The Theory of Island Biogeography proposed in 1967 brought the understanding of oceanic islands to interpret a fragmented landscape (HUBBELL; UNIFIED; THEORY, 2001). In this way, it considers a fragmented environment as a "sea" of human-dominated cover areas in which islands of native vegetation are inserted. This framework was especially important to understand the consequences of the isolation and size of remnants on biodiversity in fragmented environments. However, in contrast to oceanic environments, a fragmented landscape does not have a binary character, that is, it does not consist only of forest and non-forest environments. Contrary to the oceanic environment, the anthropic environment within a fragmented landscape is heterogeneous and presents different degrees of disturbance (HAILA, 2002).

When considering the heterogeneity of the landscape, the study of a human-dominated landscape must include the spatial arrangement of patches of native vegetation, the size of patches, as well as the different classes of anthropic cover (EWERS; DIDHAM, 2006). The study of the landscape must cover four factors that compose it: abiotic environment, biotic environment, natural disturbances, and anthropogenic disturbances (METZGER; NEOTROPICA, 2001). Understanding the fragmentation process from the perspective of these four components implies understanding the functions and heterogeneity of the landscape.

Considering a human-dominated landscape, connectivity is a key measure because population dynamics are dependent on dispersal movements for reproduction and foraging (PÜTTKER et al., 2011). Initially, connectivity was measured through structural connections between remnants, including corridors and steppingstones, and the permeability of the matrix was understood by its extension and restriction to the movement (METZGER; DDCAMPS, 1997). It was observed that these structures increase the connection between patches serving for the movement of species (BOSCOLO et al., 2008) or even corridors could also be a habitat for small mammals (FIALHO; CERBONCINI; PASSAMANI, 2017; MESQUITA; PASSAMANI, 2012).

2.2.2.3 Extinction debt

There is a time after habitat losses taken to species to answer to this disturb, and it is called relaxation time (KUUSSAARI et al., 2009). Because of this, the community measured after an event of habitat loss cannot be a real picture of the scenario after the habitat loss. The relaxation time may influence the observation of the number or proportion of populations expected to eventually become extinct, or decline, after habitat change. This proportion of the population expected to decline or become extinct in a metapopulation is the definition of extinction debt (KUUSSAARI et al., 2009).

2.2.2.4 Landscape heterogeneity

From the need to understand the environment from the perspective of the species, it was verified that the different classes of anthropic cover can have different effects on the species, not necessarily acting as a barrier to the movement of organisms (PREVEDELLO; VIEIRA, 2010b; UMETSU; PAUL METZGER; PARDINI, 2008). This raised the interest in studying the classes of anthropic cover and observing their relationship with the species. Taking permeability as a measure of the degree of percolation allowed for each land cover, it was observed that different species can use anthropic cover to a greater or lesser extent in a heterogeneous landscape (PREVEDELLO; VIEIRA, 2010b).

The relationship between species and habitat occurs in such a way that the reduction in the habitat amount results in loss of species richness (MELO et al., 2017a). This is because habitat reduction increases the propensity for colonization by invasive species (DA ROSA et al., 2017) and augments the diseases brought by domestic animals (CURI et al., 2017). This series of disturbances can lead to a process of defaunation in which, despite the presence of patches, these patches have a drastic reduction in their fauna (DIRZO et al., 2014).

2.2.3 Landscape flows and functions

Two types of flows or functions occur within a mosaic: abiotic flows, which consider wind and fire, for example, and biotic flows, which consider the movement of individuals and genetic material (FORMAN, 1995). First, considering the effect of abiotic flows on small mammals, it is necessary to understand the effect of fire dynamics on these species in the Cerrado.

2.2.3.1 Landscape flows and functions – abiotic flows

The response of the small mammal community to fire depends on the severity and extent of the fire (MENDONÇA et al., 2015). In the post-fire period, there is an increase in the species richness of small mammals in the early stages of succession (HENRIQUES et al., 2006). This recolonization depends on microhabitat and diet, being initially carried out by species of omnivorous small mammals and with fewer restrictions on microhabitat (VIEIRA; BRIANI, 2013). Considering micro-habitat issues, arboreal species from forest formations in Cerrado are more sensitive to fire than species from savanna formations (MENDONÇA et al., 2015).

2.2.3.2 Landscape flows and functions – biotic flows

There are two types of most important biotic flows or functions in the landscape that depend on its connectivity: the flow of genetic material and the movement of individuals. Gene flow consists of the transfer of new genes and genetic combinations between populations. The dispersion of individuals contributes to the maintenance of this flow (FORMAN, 1995). In small mammals, the probability of an individual dispersing is linked to its ability to perceive the environment through its sensory attributes (FORERO-MEDINA; VIEIRA, 2009), and this ability varies depending on the landscape configuration (PREVEDELLO; VIEIRA, 2010a). In this way, the spatial arrangement of the mosaic can act in a facilitating or restrictive way to the movement of species, influencing the maintenance of the genetic diversity of populations.

The movement of species within a mosaic can happen in three ways that differ essentially in their scale: at a local scale, within the species' home range, i.e., within the area it uses for foraging; at a regional scale through the dispersion that happens between populations within a landscape; or at the global scale through migration which is the cyclical movement observed as part of the dynamics of a species. The movement does not happen randomly and depends on the configuration of the mosaic, however, the perception of a pattern depends on the scale on which it is evaluated (FORMAN, 1995).

Among the movement types, small mammals move within their home range and disperse within the landscape. The home range is the foraging site of individuals. Its extent is related to body size - intraspecific and interspecific variation - and sex of individuals within a population - intraspecific variation

(SLADE; RUSSELL, 1998). It is estimated for Brazilian Cerrado rodents that the home range may vary from approximately 500 m² for species that are more demanding in terms of habitat (ALHO; PEREIRA; PAULA, 1986; GENTILE; CERQUEIRA, 1995) to 15,000 m² for habitat generalist species (ERNEST; MARES, 1986). For marsupials, it varies from approximately 12,000 m² (GENTILE; CERQUEIRA, 1995; PIRES FERNANDEZ, F. A. S., 1999; TAYLOR; BERGALLO, 1994) to 30,000 m² (CÁCERES; MONTEIRO-FILHO, 2001; D'ANDREA et al., 1999). Although a living area of 500 m² may seem like the ideal size for the study of a patch, this dimension may not necessarily be the ideal area. A specialist species demands a smaller home range (500 m²), but it is more specific in terms of microhabitats, common to large patches.

2.3 Agent-based models in landscape ecology studies

2.3.1 2.3.1 Landscape ecology and complex systems

To understand how biodiversity is affected by habitat loss, the landscape approach focuses on the spatial arrangement of patches and different types of anthropic cover (EWERS; DIDHAM, 2006; HAILA, 2002). This approach focuses on the study of four factors that compose the landscape structure: abiotic and biotic environment, and natural and anthropogenic disturbances (METZGER; NEOTROPICA, 2001). Understanding the effects of fragmentation on biodiversity based on the large number of variables that formed these components is challenging.

The great number of variables that make up a phenomenon characterizes it as a complex system. Common in Biological Sciences, complex systems are systems governed by multiple individual elements that interact with each other and whose result and behavior of these interactions are unpredictable from the elements themselves, causing an emergent phenomenon of these interactions. This emergent phenomenon is not the simple addition or subtraction of individual elements, making the interaction immeasurable (WILENSKY; RAND, 2015).

In an attempt to understand complex systems, statistical techniques emerged to deal with a complexity that until now would be characterized as a "disorganized complexity" – due to the presence of many variables of random behavior (GRIMM et al., 2005b). This is because when evaluating a large number of variables together, there is a risk of increasing uncertainties in the interpretation of this phenomenon (LAHSEN, 2005).

How to find a balance in the study of these systems between simplification and the increase in uncertainty resulting from the inclusion of many variables? One must find a balance between the patterns that represent a system and not get lost in detail that is local or has little interference in the process to be studied (GRIMM et al., 2005a). Ideally, the most relevant variables on these systems should be selected, excluding those that have little potential to act on them (GRIMM et al., 2005a; WEAVER, 1991). GRIMM et al. (2005b), evaluating studies that consider the movement of individuals, for example, suggest that by including a single observation of a single individual the probability of including behavioral peculiarities increases. This would lead to the inclusion of variables that do not represent the group. However, by increasing the sampling of individuals, patterns that represent the phenomenon can be observed, enlarging the possibility of understanding this system. In this context, modeling is a tool that allows the simulation of phenomena from a greater number of variables for the understanding of complex systems.

2.3.2 The agent-based model in the study of complex systems

The Agent-based model (ABM) emerges as a useful tool for the study of complex systems since it allows simulating the interactions based on the behavior of agents. In this modeling method, the phenomenon is understood from the agents and the interaction between them (WILENSKY; RAND, 2015). The search for patterns that reflect behavior is a way of defining the rules of agents and their interactions (GRIMM et al., 2005b). Thus, ABM makes it possible to observe both the agents compound the system as well as the interaction between them (GRIMM et al., 2005a; MATTHEWS et al., 2007) providing the knowledge of the patterns that emerge from these interactions.

An agent is defined as an autonomous computational individual whose properties and actions are inherent to itself (WILENSKY; RAND, 2015). In an ABM, more than the behavior of the agents, the model must reflect the patterns that emerge from these interactions and that characterize the system (GRIMM et al., 2005b). An ABM is composed of agents, the environment or space where agents interact, and rules, which determine the forms of interactions between agents (in this study, small mammals) and the space (VERBURG et al., 2013, p. 200). The structure of this type of model emerges from the interaction between agents and can be modeled directly. However, behavior and interactions have a dynamic character so that agents move and learn, which can cause changes in behavior patterns (GILBERT, 2008).

In general, the study through modeling techniques starts from a question to be answered and hypotheses that answer that question. Grimm et al. (2005) state that these hypotheses must be established to consider not only the patterns found but in the opposite way, it must also present scenarios that invalidate the hypothesis established a priori based on the observed patterns. This is because, many times, the behavior can emerge from the interactions observed in the simulation. This approach increases the possibility of understanding the system.

Given the need to verify the coherence of a model, the confrontation between the proposed model and the data obtained is a form of calibration and validation (GRIMM et al., 2005a). This must be done by comparing the results generated by the model and the observed patterns. The closer the results obtained through the model and the observed patterns are, the greater the understanding of the factors that act on the system. Even knowing the rules that make up a system, the patterns that emerge are difficult to predict (GRIMM et al., 2005a).

The following papers are part of the process of understanding the interactions of modeling. Chapters 3 and 4 present the understanding of land cover changes in the Cerrado, or the spatial component of this thesis model. Chapter 5 presents how was defined the scale and the choices in how to represent space in the small mammals' analysis in Chapter 6. Chapter 6 evaluates how the small mammals answer to different contexts of habitat loss and matrix predominance in the Cerrado context. Finally, Chapter 7 presents the modeling process resulting from the interactions of the landscape and the agents.

3 EFFECTS OF DEFORESTATION OVER THE CERRADO LANDSCAPE: A STUDY IN THE BAHIA FRONTIER[1]

3.1 Introduction

Economic interests as well as socioeconomic aspects, such as increased demographic density, together with programs to encourage the development and construction of high- ways, agriculture, and cattle activities can work as drivers of the agricultural frontier expansion and deforestation in tropical biomes (ESPÍRITO-SANTO et al., 2016; LAURANCE; SAYER; CASSMAN, 2014; METZGER, 2009). The Tropical Savanna Biomes (TGB— Tropical Grassy Biomes) are the biomes that include savannas and grasslands. Those biomes are under pressure due to land cover changes that affect biodiversity and biogeo- chemical cycles (LEHMANN; PARR, 2016). Inserted in this context, the Cerrado, or the Brazilian Savanna, also faces deforestation impacts over its native area (KLINK; MACHADO, 2005).

The Cerrado is an open domain biome with the most representative extension in South America, and due to its number of species, endemism (approximately 4,800), and threat suffered by these areas it is considered a "biodiversity hotspot" (BRASIL, 2014; MYERS et al., 2000b). In addition to its biodiversity importance, the Cerrado is highly relevant for the balance of biogeochemical cycles, maintained by their fire regimes. Also, this region is important for its high popula- tion concentration (approximately 46 million inhabitants) and the expressive agricultural production in its territory (approximately 17.43 Mha of the three main products, soy, corn, and cotton, in 2014) (BOLFE et al., 2016; LEHMANN; PARR, 2016). The region known as MATOPIBA that corresponds to the states of Maranhão, Tocantins, Piauí, and Bahia had a population

---

[1] Based on: ASSIS, T. O.; ESCADA, M. I. S.; AMARAL, S. Effects of deforestation over the cerrado landscape: A study in the Bahia frontier. **Land**, v. 10, n. 4, p. 1–15, 2021.

estimated at 5.9 million people and produced approximately 2.2 Mha of soy, corn, and cotton in 2016 (BOLFE et al., 2016).

Until 2013, the Cerrado lost approximately 50% of its native cover to human use (SCARAMUZZA et al., 2017). Recent data also show that the biome still presents areas of agricultural expansion over native vegetation in its interior [10]. Between August 2019 and July 2020, 7340 km2 of native vegetation was removed, an increase of 13% concerning the losses observed in the previous 12 months (6483 km2) (BEUCHLE et al., 2015). Some studies report that the losses in Cerrado native cover are increasing fragmentation (CARVALHO; DE MARCO; FERREIRA, 2009a). The losses in the native cover in Cerrado have also been reported to affect the carbon stock and the biodiversity in this biome (COELHO et al., 2020). This process can be aggravated with the expansion of agriculture in addition to weak policies of conservation (COELHO et al., 2020; FRANÇOSO et al., 2015; ROSA, 2021).

Currently, the Cerrado scenario presents a low number of areas destined for conservation. Agricultural expansion motivated by speculation in land prices, lack of a policy to control the losses of native cover, and incentives for agribusiness as an economic model will lead to a reduction in the number of native remnants and a decrease in connectivity in the landscape (STRASSBURG et al., 2017). In contrast, removing the pressure over native areas would allow connectivity in the landscape to be maintained, or restored by the regeneration of native Cerrado (STAN et al., 2015). Maintaining the landscape with a greater number of remnants and high connectivity is essential for maintaining biodiversity (BARRETO et al., 2012). The Cerrado has a large number of threatened species, 307 species on the Red List (BRASIL, 2014), and the immediate threat to native vegetation due to losses from agricultural expansion. In addition to these factors, the Cerrado still contributes to environmental services, maintaining soil moisture and carbon cycling (BATLLE-BAYER; BATJES; BINDRABAN, 2010; STAN et al., 2015).

The conversion of native areas into anthropogenic land covers can result in a fragmented landscape with sparse remnants of native vegetation, distributed within a mosaic with a predominance of anthropic land coverages. The fragmentation process over the original vegetation results in a decrease in patch areas and an increase in edge areas and the number of patches (FAHRIG, 2003). The habitat loss and consequent fragmentation due to this process have a negative effect on biodiversity, but the fragmentation per se, which means in the same habitat amount, has a mostly null effect on biodiversity (FAHRIG, 2017, 2019; FAHRIG et al., 2019). However, the null effect of fragmentation per se on biodiversity is not a consensus in the literature (FLETCHER et al., 2018; MILLER-RUSHING et al., 2019; PÜTTKER et al., 2020). Despite this controversy about the effects of fragmentation, the measure of losses in native cover and fragmentation per se must be in the landscape scale (FAHRIG, 2019).

The choice of the most appropriate scale to represent the landscape mosaic should consider the gains and losses to observe the object of analysis on a local and global scale (MEENTEMEYER, 1989; TURNER, 1989). Local scale allows for the production of accurate local information but also makes it difficult to generalize the results found due to local particularities. On the other hand, in landscape mosaics studies, local scale can hide the heterogeneity of the landscape. A global-scale analysis enables broader approaches, but it is more susceptible to inaccuracies due to the suppression of elements that are not visible in their representation (SEPPELT; LAUTENBACH; VOLK, 2013).

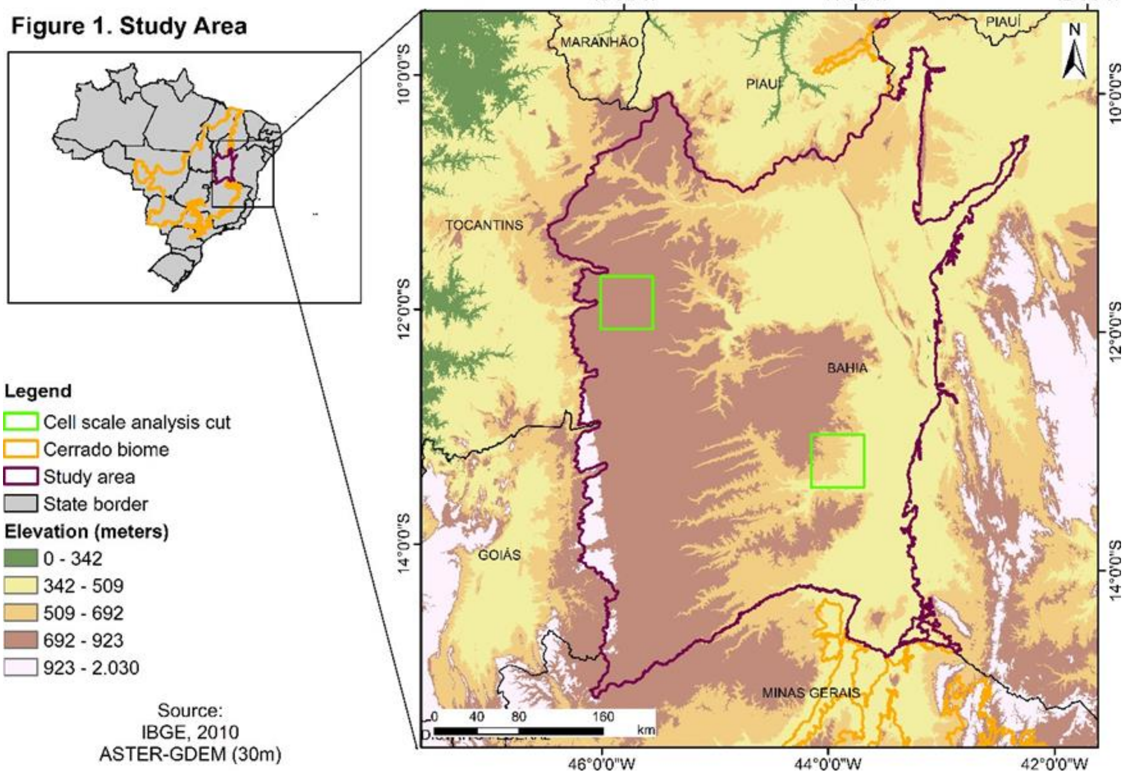
It has been well-recorded that the Cerrado is losing its native areas over the years and that agricultural lands are increasing (ALENCAR et al., 2020). An increase in fragmentation of native Cerrado has also been reported over the years (CARVALHO; DE MARCO; FERREIRA, 2009a). However, it is fundamental to understand where, considering the landscape structure, this process is preferably occurring, and how it relates with the landscape context to develop policies in both preventing the impact and promoting conservation. It is also utterly important to verify if the losses in native cover are increasing the fragmentation in order to establish a protection mechanism not only to continuous native cover but also to small patches (FAHRIG, 2020). Considering the presented context, this work poses the following specific questions: How does the deforestation process change the landscape structure (or landscape patterns) in the Brazilian Cerrado, and where do the losses of native Cerrado occur in the landscape context? We used these questions to describe the methodology and results. To answer these questions, we considered the Cerrado located in the western region of the state of Bahia—a representative area of the active agricultural expansion frontier. We used landscape metrics, and land use and land cover (LULC) data from 2013 and 2020 to quantify the changes in the landscape. Then, we proposed a typology of landscape patterns to classify and characterize the Cerrado land- scapes and to understand where the processes of change are occurring. We quantified and discussed the changes for each landscape pattern in the study region, from 2013 to 2020.

3.2 Material and methods

3.2.1 Study areas

The study area is the Cerrado biome in the state of Bahia, with a total area of 151,167 km2, corresponding to approximately 27% of its entire territory (Figure 3.1). The region has an average annual rainfall of 1500 mm and an average annual temperature of 24 ◦C (SPERA et al., 1999). Deep soils predominate in the region, a pedological characteristic that added to the geomorphological formation of the plateau and makes the region propitious to the development and mechanization of agriculture (SPERA et al., 1999). In 2020, the region concentrated 919.15 km2 of deforestation increment. According to TerraClass Cerrado data (SCARAMUZZA et al., 2017), the study area has a predominance of natural vegetation that totals 66.78% of the area. The second and third most representative uses of the study area are, respectively, pastures (16.17%) and croplands, considering annual and perennial croplands (14.82%).

Figure 3.1. Study area–Cerrado biome in the state of Bahia, Northeastern Brazil with altimetry.



Source: The author.

3.2.2 Database

We used the TerraClass Cerrado LULC map, referring to 2013, as the base for the development of the landscape typology for the study area. The TerraClass Cerrado project (an INPE, EMBRAPA, IBAMA, UFU, and UFG partnership) provides data on land use and land cover from Landsat 8 satellite images and takes 6.25 hectares as the minimum mapping area. This project used a semi-automatic classifier combined with visual interpretation to map the classes: annual croplands, perennial croplands, pastures, forestry, mosaic of occupation, urban, mining, bare soil, natural, natural without vegetation, water, and non-identified (clouds and burned areas) (STRASSBURG et al., 2017).

In the absence of a recent LULC mapping compatible with the TerraClass Cerrado of 2013, we adopted an alternative approach to map and quantify the effect of deforestation over the Cerrado landscape. Thus, we used maps provided by PRODES Cerrado to quantify the changes in the native cover of the Cerrado from 2013 to 2020. PRODES Cerrado is a project whose objective is mapping the deforestation inside the Cerrado biome. Its first mapping product is referred to the year 2000, and it mapped the land cover classes: native vegetation, anthropic, water, and not observed (clouds and shadows). Since then, every year, PRODES maps the increment in anthropic areas, considering as anthropic those areas of deforestation, regardless of the intended use (BRITO et al., 2018). PRODES Cerrado deforestation mapping results in a yearly increment of deforestation, always taking the previous year as the reference. The data is obtained using as sources images from TM/Landsat5, ETM+/Landsat7, OLI/Landsat8, and LISS-III/RESOURCESAT2.

3.2.3 How does the intense deforestation process change the landscape structure (or landscape patterns) in the brazilian Cerrado?

To answer this question, we first quantified the native Cerrado cover (class natural) in the LULC map from 2013 and 2020 in the study area. To quantify the Cerrado native cover in 2020, we subtracted the deforestation of 2013 to 2020 from the class natural on the TerraClass Cerrado map from 2013 and used the new map obtained with the results of the class natural as a reference to 2020. Then, we computed landscape metrics of fragmentation for 2013 and 2020 to verify if the changes in the amount of Cerrado native cover increased the fragmentation in the area. We chose as fragmentation metrics the number of natural patches (Patches Number), the total edge (Total Edge), and the mean of patch size (Mode Area). The choice of these fragmentation metrics (Patches Number, Total Edge, and Mode Area) followed Fahrig (2017) who stated that these are the best metrics to measure fragmentation because it is possible to control their relationship to habitat amount. We used the vector data to obtain all metrics using the ArcGIS Desktop. The Patches Number is the sum of natural patches in the whole study area. The Total Edge is the sum of the natural patches perimeters in the whole study area. Finally, we obtained the Mode Area value, calculating the area of each natural patch, and then obtained the mode value for the study area.

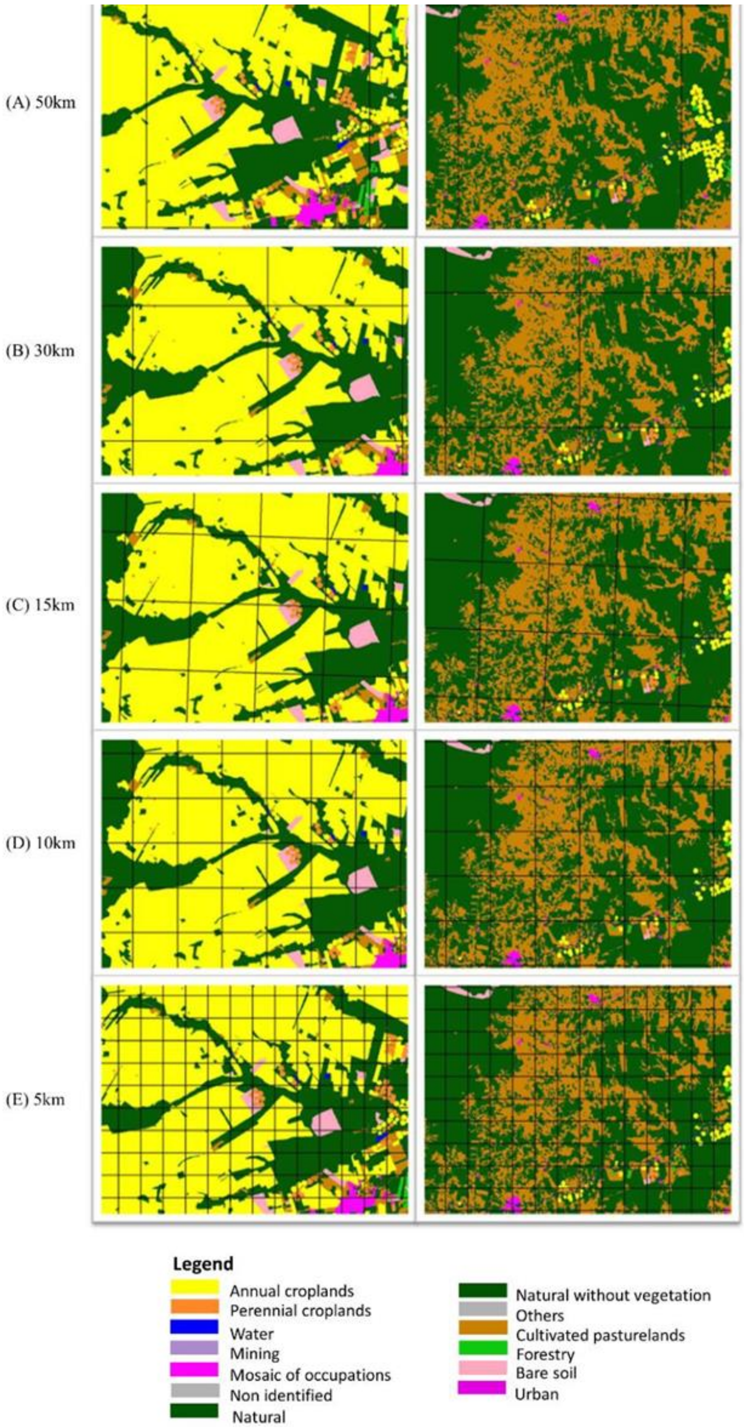
3.2.4 Where do the losses of Cerrado native cover occur in the landscape context?

To answer this question, we used the LULC map first as a reference to build the landscape typology, and then as input to classify the region. Next, we characterized each landscape type by computing landscape metrics over the LULC map, using all classes from TerraClass Cerrado 2013. After we classified the landscape in types, we quantified the changes in the Cerrado native cover in each type using the 2020 map. A detailed description is provided in the following subtopics.

3.2.4.1 Landscape typology and description

We built a regular grid for the study area, in which we considered each cell grid as a landscape unit. To choose the best scale, we assessed the scale necessary to analyze the object of this study, as suggested by Meentemeyer (1989): the landscape patterns. We chose a cell size in which most cells had some level of heterogeneity, ensuring that the patches of Cerrado native cover, the object of this study, were present in most of them, making it possible to characterize the Cerrado fragmentation process in each land mosaic category. This choice considered the scale of analysis in greater detail, involving an analysis of the landscape structure and composition. The empirical (visual) process enables not only the analysis of the dimensions of the features of interest present in the LULC map but also includes the criteria of cell homogeneity concerning the structure and composition of the landscape. This way, we defined the cell size empirically from the analysis of the polygons of interest where it was possible to observe the distinct patterns of different classes, and the patch sizes, present in the landscape. For the empirical analysis, we selected two cuts in the study area (Figure 3.1) to analyze the different scales (Figure 3.2). The choice of these areas was appropriate to obtain different patterns in the landscape.

Figure 3.2. TerraClass 2013 land use and land cover (LULC) map in the study area and different cell size: (A) 50 km; (B) 30 km; (C) 15 km; (D) 10 km; (E) 5 km. On the left, a region with a predominance of large LULC areas, and the right, a region with a predominance of small LULC areas.

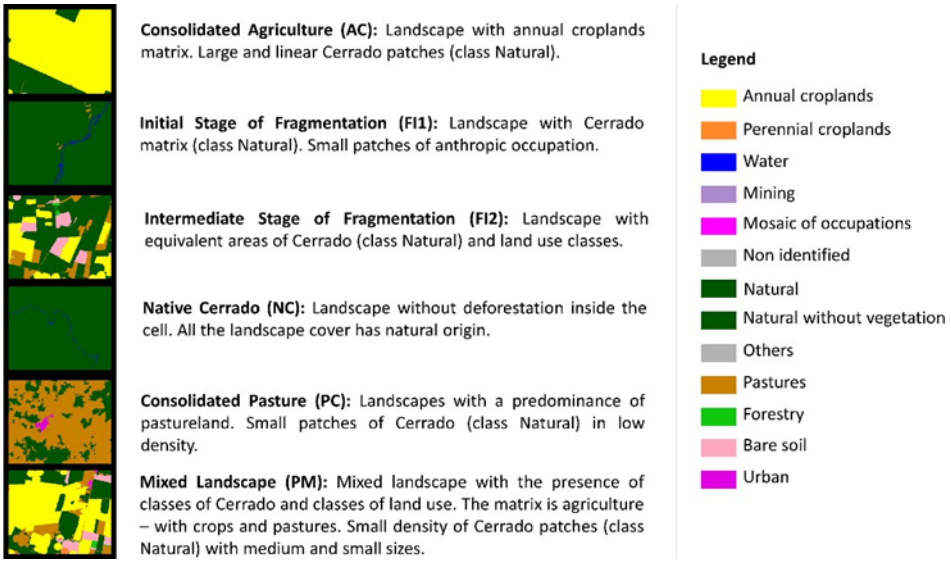


Source: The author.

Evaluating cell sizes with sides 5 × 5 km, 10 × 10 km, 15 × 15 km, 30 × 30 km, and 50 × 50 km, (Figure 3.2), we found that 15 × 15 km was the most appropriate cell size. It is possible to observe in Figure 2 that even though the biggest cell sizes (50 km and 30 km) allowed for the proper representation of the pattern of large polygons (right side), they are not appropriate to represent small polygons (left side), because they generalize the land cover patterns in those landscapes. Conversely, the smallest cell sizes (5 km and 10 km) are not able to detect heterogeneity in landscapes with large polygons (right side). Thus, we chose the intermediate cell size (15 km) because it was able to detect the landscape heterogeneity with large and small polygons. Considering this, we built the grid with cells of 15 km × 15 km for the study area. Each grid cell contained land use and cover classes from the LULC TerraClass Cerrado mapping. This procedure aims to redistribute the LULC data to a cellular space considering a homogeneous matrix of cells.

For the typology, we defined the types a priori based on the land cover class patterns observed and their frequency in the landscape. Considering the predominant type of coverage in the cell, we defined five typologies: Consolidated Agriculture (AC), Initial Stage of Fragmentation (FI1), Intermediate Stage of Fragmentation (F12), Native Cerrado (NC), Consolidated Pasture (PC), and Mixed Landscape (PM), as presented and described in Figure 3.3.

Figure 3.3. Landscape typology of patterns observed in the study region from the composition and arrangement of TerraClass Cerrado land use and land cover patterns.



Consolidated Agriculture (AC): Landscape with annual croplands matrix. Large and linear Cerrado patches (class Natural).

Initial Stage of Fragmentation (FI1): Landscape with Cerrado matrix (class Natural). Small patches of anthropic occupation.

Intermediate Stage of Fragmentation (FI2): Landscape with equivalent areas of Cerrado (class Natural) and land use classes.

Native Cerrado (NC): Landscape without deforestation inside the cell. All the landscape cover has natural origin.

Consolidated Pasture (PC): Landscapes with a predominance of pastureland. Small patches of Cerrado (class Natural) in low density.

Mixed Landscape (PM): Mixed landscape with the presence of classes of Cerrado and classes of land use. The matrix is agriculture – with crops and pastures. Small density of Cerrado patches (class Natural) with medium and small sizes.

Source: The author.

From the proposed typology, we collected samples of each landscape type. From those, 66% of the samples were training samples and 34% were test samples. Then, we classified the region using the Decision Tree in GeoDMA (KÖRTING; GARCIA FONSECA; CÂMARA, 2013). The C5.0 Decision Tree from GeoDMA used in this study is the implementation of the Quinlan's C5.0 Algorithm. This supervised classification method uses attributes in the training records to assemble a tree, ignoring cases with bad or unknown classes. We did not establish initial limit parameters for decisions among classes for the samples; we selected the training samples visually and we used them to classify the cells. The landscape metrics thresholds define each branch of the tree, resulting in the distinction of classes and the classification of the typology map.

To build the decision tree and to classify the region, we used as attributes the following landscape metrics, obtained from the LULC map from TerraClass Cerrado: the percentage of each class (annual croplands, perennial croplands, pastures, forestry, mosaic of occupation, urban, mining, bare soil, natural, natural without vegetation, water, and non-identified), the number of natural patches (Patches Number), the total length of the edge of the natural patches (Total Edge) and the mode value of the natural patch size inside the cell (Mode Area). To obtain the percentage of each class, we used the total area of each class inside each cell divided by the total cell area. The Patches Number is the sum of natural patches inside each cell. The Total Edge is the sum of the natural patches perimeters inside the cell. Finally, we obtained the Mode Area, calculating the area of each natural patch in the cell, and then computed the mode value for the cell. We used the vector data to obtain all metrics using the ArcGIS Desktop.

We chose these fragmentation metrics (Patches Number, Total Edge, and Mode Area) following Fahrig (2017), who stated that these are the best metrics to measure fragmentation because it is possible to control their relationship to habitat amount. After classification, the selected test samples from each class were used to verify the mapping accuracy by calculating the Kappa Index based on the confusion matrix. After the classification, we used the metrics to describe each type of landscape.

3.2.4.2 Landscape changes in Cerrado native area

To characterize the landscape changes from 2013 to 2020, we used the yearly deforestation map from 2013 to 2020 provided by PRODES Cerrado and subtracted from the class natural of the LULC map of TerraClass Cerrado to obtain the Cerrado native cover in 2020. Using the Cerrado native cover of 2020, we computed the metrics, previously defined, to characterize the landscape structure for each type from the classification obtained in 2013: the percentage of Cerrado native cover (Percentage Native Area), Patches Number, Total Edge, and the Mode Area.

To verify how the Cerrado landscape changed between 2013 and 2020, we performed a statistical analysis to compare the Cerrado native cover in each type of landscape (AC, FI1, FI2, NC, PC, and PM) in 2013 and 2020. First, we used the Shapiro-Wilk to test the data normality. After testing normality, we used the T-test for parametric data and Wilcoxon test for non-parametric data, to test if the Percentage of Native Areas were different inside each landscape type between 2013 and 2020. When we found a difference in the Percentage of Native Area, we also tested the difference for each metric (Patches Number, Total Edge, and Mode Area) between 2013 and 2020, using the same tests.

3.3 Results

3.3.1 How does the intense deforestation process change the landscape structure (or landscape patterns) in the brazilian Cerrado?

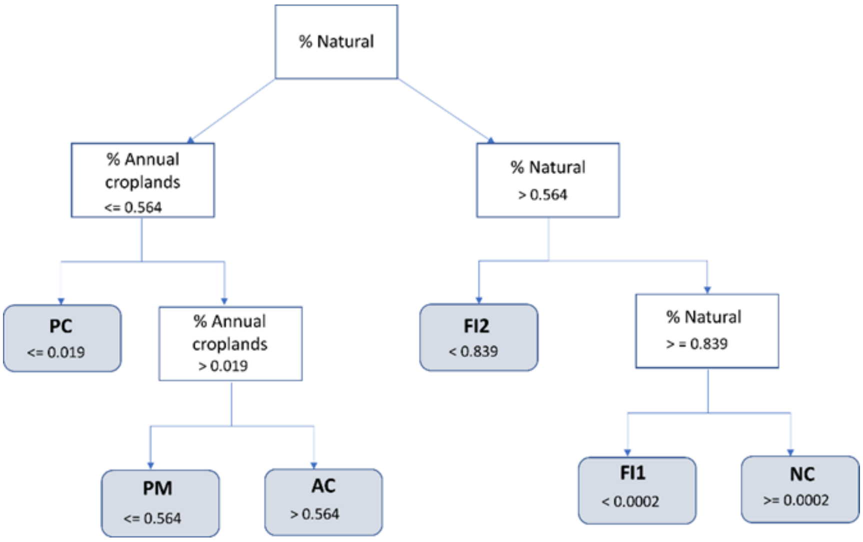
From 2013 to 2020, the percentage of native cover decreased by 3.85% in the Cerrado biome in the state of Bahia. In 2013, the percentage of Cerrado native cover in the study was 66.78% (102,086.41 km2) and it decreased to 62.93% (96,193.81 km2) in 2020. The Mode Area decreased from 8.09 km2 in 2013 to 8.43 km2 in 2020. We observed a decrease in the Number of Patches from 2013 (11,464) to 2020 (11,402). The Total Edge increased from 128,246.63 km in 2013

to 147,133.07 km in 2020.

3.3.2 Where do the losses of Cerrado native cover occur in the landscape context?

The decision tree used the percentage of Cerrado native cover (natural class) in each cell as the first attribute to separate the types. In the first branch were the cells in which the percentage of natural was <= 56.48 %. In the first branch, when the percentage of annual croplands was <= 1.92 % the cells were classified as PC; cells with the percentage of annual croplands > 1.92 % and 56.44 % were classified as PM; and cells with the percentage of annual croplands > 56.44 % were classified as AC. The second branch separated those cells where the percentage of natural class in each cell was > 56.48 %. When the percentage of natural was <= 84.0% the cells were classified as FI2; when the percentage of natural was > 84.0% and < = 0.02% the cells were classified as FI1; and when the percentage of natural was > 0.02% the cells were classified as NC (Figure 3.4).

Figure 3.4. Decision tree used to classify the Cerrado landscape classes in the state of Bahia. Consolidated Agriculture (AC), Initial Stage of Fragmentation (FI1), Intermediate Stage of Fragmentation (F12), Native Cerrado (NC), Consolidated Pasture (PC), and Mixed Landscape (PM).



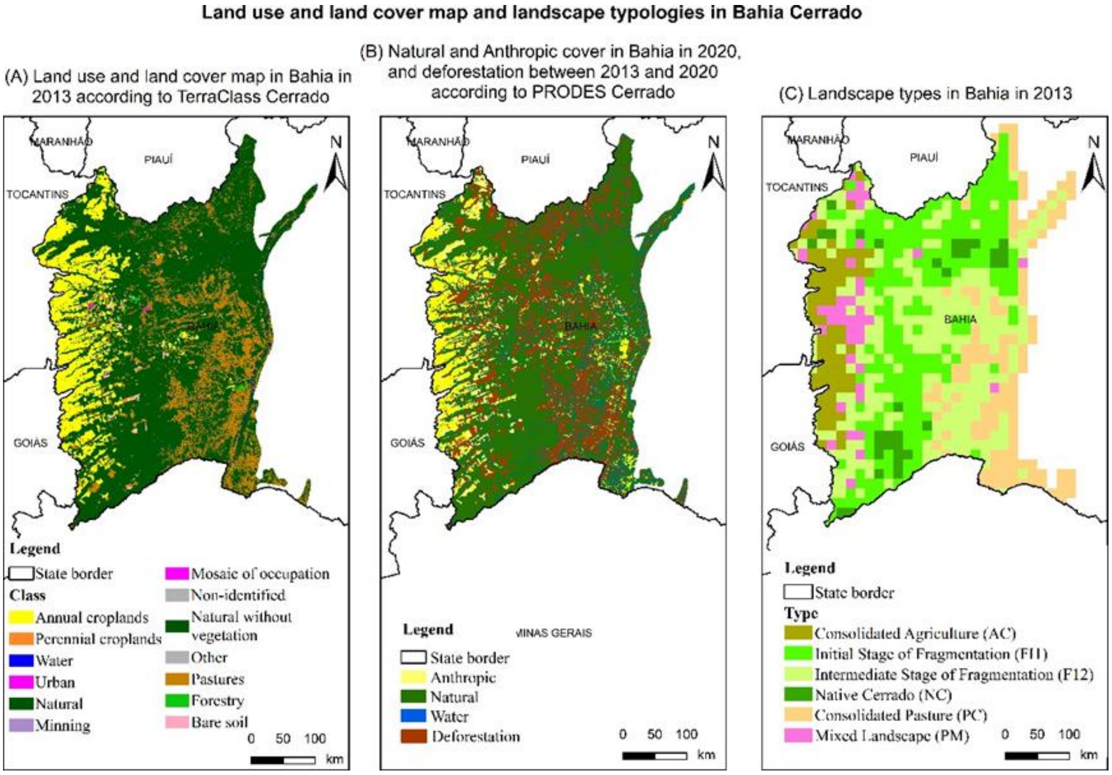
Source: The author.

In the study area, the predominant landscape in 2013 was FI2 (32.53%), followed by FI1 (31.26%), PC (16.4%), AC (89.78%), PM (5.59%), and NC (4.70%) (Figure 3.5). Based on test samples, the general map accuracy was 88.2%, and the confusion matrix is presented in Table 3.1.

Table 3.1. Confusion matrix of training samples and test samples used to classify the landscape typology of the Bahia Cerrado region.

	Size = 6						**Size = 6**					
	Errors = 1 (0.9 %)						**Errors = 2 (3.8 %)**					
	Training Sample Evaluation (n=109)						**Test Sample Evaluation (n=53)**					
	AC	**FI1**	**FI2**	**NC**	**PC**	**PM**	**AC**	**FI1**	**FI2**	**NC**	**PC**	**PM**
AC	14						13					
FI1		21						6				
FI2			17						9			1
NC				20						7		
PC					20						7	
PM	1					16	1					9

Figure 3.5. Land use and land cover in Bahia according to TerraClass Cerrado 2013 data, and classification of landscape typologies in the Cerrado of Bahia.

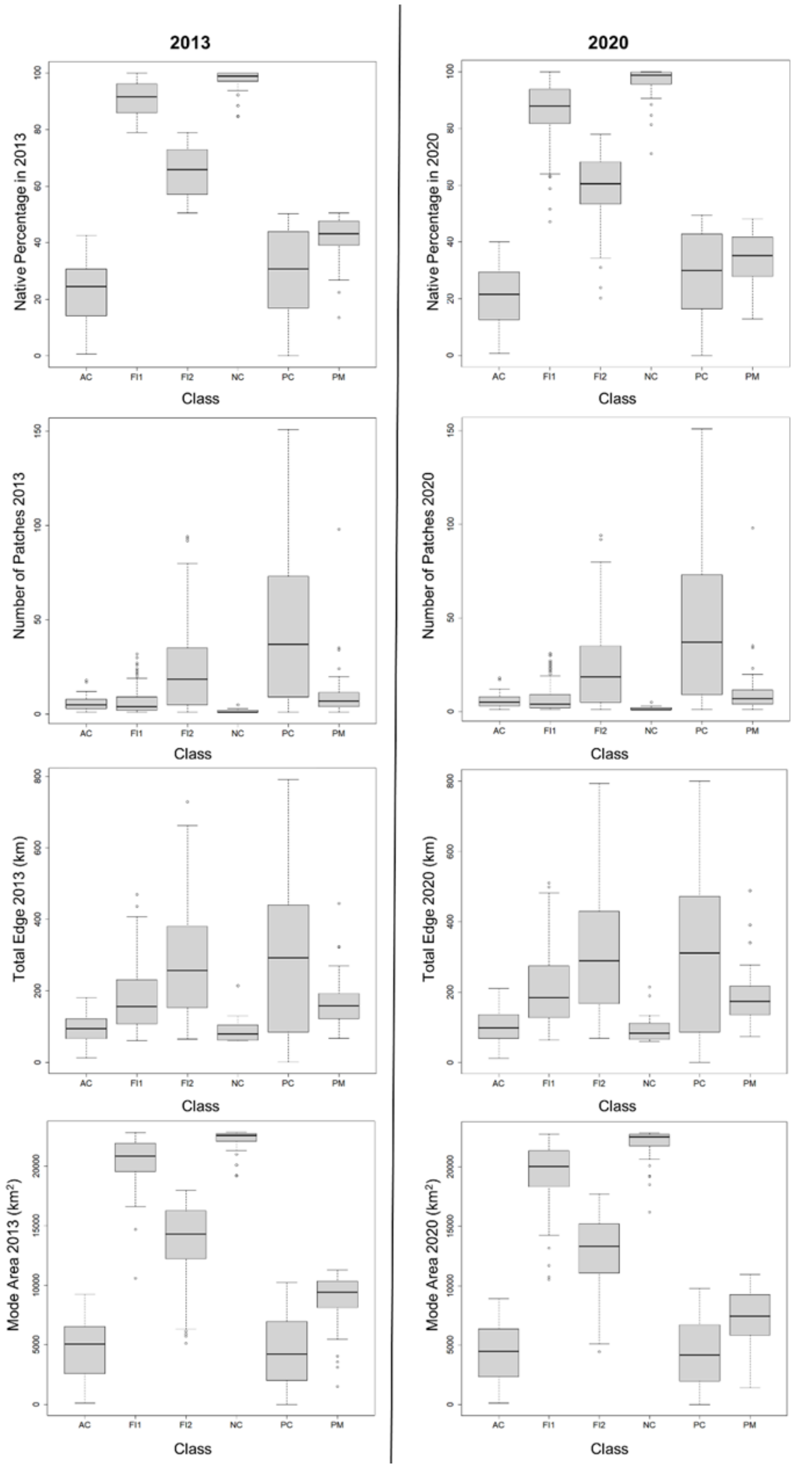


(A) Land use and land cover map in Bahia in 2013 according to TerraClass Cerrado: LULC map in the state of Bahia according to TerraClass Cerrado 2013 data. (B) Natural and anthropic cover map in Bahia in 2020 according to PRODES Cerrado: the map shows the natural cover and all anthropic covers represented by the class anthropic in 2020 according to PRODES Cerrado. (C) Landscape types in Bahia: Typology map in the state of Bahia obtained from the decision tree classification.

Source: The author.

The percentage of Cerrado native cover was higher inside NC, followed by FI1, FI2, PM, PC, and AC for 2013 and 2020. The Total Edge and the Number of Patches were higher inside PC, FI2, PM, and FI1, followed by AC, in both years. The Mode Area was higher inside NC, followed by FI1, FI2, and PM. PC and AC had the smallest Mode Area. We also observed this pattern in 2013 and 2020 (Figure 3.6).

Figure 3.6. Boxplot of the metrics Native percentage of Cerrado, Patches Number, Total Edge, and Mode Area for each landscape type (AC, FI1, FI2, NC, PC and, PM), in 2013 and 2020.



Source: The author.

From the results of the Wilcoxon test (W) and T-test (T and p-values), when comparing the difference in the native percentage of the Cerrado between the years 2013 and 2020, the classes FI1 (W = 37502, p-value = 4.351×10−6), FI2 (W = 41703, p-value = 9.408×10−8), and PM (W = 1476, p-value = 1.311 × 10−5) showed significative differences in Native Cerrado percentages. The classes NC (W = 770, p-value = 0.3579), AC (W = 770, p-value = 0.3579), and PC (W = 8448, p-value = 0.513) did not show a difference in the native percentage of the Cerrado between the years 2000 and 2013.

We tested the difference in the landscape between 2013 and 2020 for FI1, FI2, and PM because they showed differences in the percentage of Native Cerrado (Table 3.2). There was no significative difference in the Number of Patches in FI1 (W = 30388, p-value = 0.934), FI2 (W = 32918, p-value = 0.929), or PM (W = 970, p-value = 0.990) between 2013 and 2020. There was significative difference in Total Edge in the landscapes FI1 (W = 25056, p-value = 0.001) and F12 (W = 28592, p-value = 0.012), while there was no significative difference in Total Edge for the landscapes PM (W = 844, p-value = 0.304) between 2013 and 2020. The Mode Area was significative different in FI1 (W = 37152, p-value = 1.233 × 10−5), FI2 (t = 4.1624, df = 510, p-value = 3.696 × 10−5), and PM (W = 1392, p-value = 0.0003221) between 2013 and 2020.

Table 3.2. Results of the metrics inside FI2 in 2013 and 2020 average values: Percentage of Native cover, Number of Patches, Total Edge, and Mode Area.

Landscape Pattern	Landscape Metric	Year 2013	Year 2020
FI1	Percentage of Native cover (%)	63.44	59.87
	Number of Patches	6.19	6.24
	Total Edge (km)	213.67	238.66
	Mode Area (km^2)	20,850.74	20,029.29
FI2	Percentage of Native cover (%)	65.21	60.43
	Number of Patches	22.97	22.82
	Total Edge (km)	275.70	310.34
	Mode Area (km^2)	14,323.71	13,328.54
PM	Percentage of Native cover (%)	41.50	34.21
	Number of Patches	11.09	11.00
	Total Edge (km)	169.58	184.12
	Mode Area (km^2)	9,431.91	7,435.12

Note: Mean from all cells.

3.4 Discussion

The Cerrado native areas are dominant in most of the Bahia Cerrado region in both the observed years, 2013 and 2020. However, the native cover decreased over time and therefore, we observed a decrease of the Mode Area, a decrease in the Number of Patches, and an increase of Total Edge in the whole area. Answering our first question, the deforestation processes affect the landscape structure in the study area by reducing the size and number of patches and increasing the amount of edge in the area. This result highlights the importance of this region to preserve the biome, since the Cerrado native cover is still dominant in the region, the opposite found for the entire biome (BARRETO et al., 2012).

The losses in the native cover in the northern Cerrado have been reported in other studies (ALENCAR et al., 2020; DE OLIVEIRA et al., 2017), but the typology map made it possible to understand in the finest resolution where the losses in Cerrado native cover are happening and to relate them to landscape patterns. Our typology map showed that NC occupies approximately 4.7% of the whole area. This result means that most of the landscape has at some level, the presence of anthropic activity. Answering the question of where the losses of native Cerrado occur in the landscape context, we observed that the losses in the Cerrado native cover were significative in the Initial (F1) and Intermediate Stage of Fragmentation (FI2), and Mixed Landscape (PM). These three types of landscape together correspond to approximately 69.38 % of the study area. We also noticed that, except for PM, the losses of native Cerrado were concentrated in FI1 and FI2, the immediate border with NC (Figure 5). PM was the only landscape type with an anthropogenic matrix where the losses in the Cerrado native cover were significative. This can be explained by the fact that among the types with an anthropogenic matrix (AC, PC, and PM), PM had the highest percentage of Cerrado native cover in 2013.

It is common for a process of habitat loss to be associated with habitat fragmentation by increasing the patches number and the total edge and decreasing the patches sizes (FAHRIG, 2003). Even though regions classified as FI1, FI2, and PM presented a lower percentage of Cerrado native cover in the landscape in 2020 than in 2013, this was not followed by an increase in the Patches Number inside them. Surprisingly, this metric was similar for both years. However, the losses in the Cerrado native cover showed the strongest effect in the patches size. We observed that the losses in the Cerrado native cover affected the area of the patches, reducing them over time, but it did not affect the number of patches in the landscape. The pattern of increasing the Total Edge happened inside the FI1 and FI2 types but did not occur in PM. Even though all areas analyzed (FI1, FI2, and PM) presented significative differences in patch size, the loss of area can have different effects on a patch's shape (FORMAN, 1995). This fact can explain such a difference in the response of Total Edge to losses in area for those landscapes.

The LULC map highlighted two regions bordering the Cerrado: the livestock frontier advancing from the east side, as observed by PC type, and agriculture crops, or AC type, from the west side (Figure 5B). In consolidated landscapes, PM has higher values of Mode Area than AC and PC. This means that when the anthropogenic matrix is not dominated by one land use in the study area, the patches are bigger than in a homogeneous landscape. Considering the fragmentation metrics, we found that PC has the highest values of Number of Patches and Total Edge.

These findings indicate that landscapes with a pasture matrix are more fragmented than landscapes with a cropland matrix. This pattern of higher fragmentation inside land- scapes with a pastures matrix is different from a study in the Cerrado in the Goiás state in 2009 (CARVALHO; DE MARCO; FERREIRA, 2009a) that found high fragmentation rates in landscapes with a croplands matrix. Compared to the pastures matrix (PC), we found fewer patches of Cerrado inside landscapes with a croplands matrix (AC), as observed by the metric Number of Patches (Figure 6). This is probably because mechanized agriculture requires large and continuous lands to occur, limiting the Cerrado areas to places where the slope and hydrography does not allow for the use of machinery (MARTINELLI et al., 2010).

After considering the amount of Native Cerrado and fragmentation, another fact to consider is the matrix heterogeneity. This is important because different matrix cover has different degrees of obstruction to native species movement (PREVEDELLO; VIEIRA, 2010b). This factor is aggravated by the present homogeneity in the matrix inside the consolidated areas (AC, PC, and PM), in which, the type of matrix is less varied. This can be seen from the fact that among the landscape types with an anthropogenic matrix (PC, AC, and PM), the class Mixed Landscape (PM) is the type with the lowest area representativeness in the study site.

We could observe that the losses in native cover of the Cerrado do not occur in consolidated landscapes (AC and PC) or inside the continuous areas of Cerrado (NC). Instead, it appeared to be a process that occurs over the landscapes with a higher percentage of Cerrado native cover and some amount of land use inside it. We could also observe this by the fact that AC, PC, and NC did not have a significative difference in the percentage of native cover. Today, the Cerrado has only 6.5% of its total area inside protected areas, allowing losses over its native area (GANEM; DRUMMOND; FRANCO, 2013).

As far as we observed, the conversion of native cover resulted in a reduction in the Mode Area and an increase of Total Edge in the area, but it did not show a difference in the Number of Patches. This finding means that the losses of native cover are happening by reducing the size of large patches and not by removing the small ones, a process different from that reported for the Atlantic Rainforest, as an example (RIBEIRO et al., 2009). This evidence plays an important role in designing conservation policies, by understanding the patterns of native cover loss and fragmentation (FLETCHER et al., 2018).

3.5 Conclusions

The Cerrado landscape in the state of Bahia has a higher percentage of areas at an early stage of fragmentation than areas at more advanced stages. However, because of anthropic use, the region of consolidated occupation presents a low density of Cerrado patches. These findings urge the need to preserve the few contiguous fragments of this biome that have the function of preserving its natural processes.

The dominance of a single type of anthropic matrix, annual croplands, or pastures over extensive areas is evident. This matrix homogeneity reduces the permeability of the landscape in the consolidated areas. Therefore, the importance of maintaining patches of native vegetation is once again emphasized.

Cerrado deforestation in Bahia also has a particular landscape pattern of natural vegetation loss. These losses are reducing large patches inside landscapes with initial and intermediate levels of fragmentation and inside landscapes with a heterogeneous matrix. Understanding the patterns of native cover loss and fragmentation is essential when designing conservation policies for Cerrado.

Finally, this article also provides a methodological contribution toward the construction of typologies - a useful tool to assess diverse landscapes, enabling us to compare heterogeneous environments or temporal evolution. From the classification of landscape patterns, one can assess fragmentation by analyzing their metrics and identifying differences in the landscape patterns. This type of approach under the landscape bias may be key to understanding the ecology of species since the spatial configuration of the remnants can determine the flow of individuals and the persistence of populations in a fragmented environment.

4 EFFECTS OF AGRICULTURE TYPE AND CONSERVATION POLICY ON LOSS AND FRAGMENTATION OF NATURAL HABITATS IN BRAZILIAN CERRADO

4.1 Introduction

The loss of natural habitats in Brazil is an important conservation challenge because Brazil has disproportionately high biodiversity. Brazil has the biggest tropical forest in the world, Amazonia, and two other biomes that are considered hotspots for biodiversity conservation: the Atlantic Forest and the Cerrado (MYERS et al., 2000a). Brazil has lost 61 Mha (10%) of its natural habitats over the last three decades (SOUZA et al., 2020). This has resulted in an increasing number of threatened species; of Brazil's 117,096 known animal species, 1,173 are currently threatened and of its 43,478 known plant species 2,118 are threatened (BRASIL, 2014).

In this context, the Brazilian savanna biome, or the Cerrado, is important for several reasons. First, the Cerrado is the biome with the greatest potential area for the legal expansion of agribusiness; around 40% of its current natural area can be legally converted to agriculture (STRASSBURG et al., 2017). Second, the Cerrado is currently losing habitat at a rate second only to the Caatinga in Brazil (RATTER; RIBEIRO; BRIDGEWATER, 1997b; SOUZA et al., 2020). Third, the Cerrado hosts the headwaters of eight of the twelve major water basins in South America (LAHSEN; BUSTAMANTE; DALLA-NORA, 2016). Finally, the Cerrado has high regional diversity, which means that an effective conservation strategy for this biome will be challenging, requiring a wide distribution of habitat protection across the biome (RATTER; RIBEIRO; BRIDGEWATER, 1997b).

Over the past few decades, there has been a significant loss of natural habitat in the Cerrado. These habitats vary from grasslands to savanna to forests, with trees from 5 to 8m (RATTER; RIBEIRO; BRIDGEWATER, 1997b). The original composition of the Cerrado, before any land conversion, was 10% grassland, 55% savanna, and 35% forest (MCTIC, 2019). The natural habitat has been reduced to approximately 50% of the total area of the biome (SCARAMUZZA et al., 2018; SOUZA et al., 2020). Of the three major natural habitat types, the rate of forest loss is highest at 0.7% per year, with 23% lost between 1985 and 2017 (ALENCAR et al., 2020; CARVALHO; DE MARCO; FERREIRA, 2009a; RATTER; RIBEIRO; BRIDGEWATER, 1997b). Over the same period, 18% of savanna and 8% of grassland were lost (annual loss rates of 0.5% and 0.2%, respectively) (ALENCAR et al., 2020). The main causes of natural habitat loss in the Brazilian Cerrado are financial incentives for human occupation; the expansion of the road network in mid-west Brazil between the 1950s and 1960s; and the expansion of farming after the 1970s for crops and pastures (CARVALHO; DE MARCO; FERREIRA, 2009a; RATTER; RIBEIRO; BRIDGEWATER, 1997b; SOUZA et al., 2020). This agricultural expansion was facilitated by new genetic strains of crops and livestock, fertilizer application, and mechanization (CARVALHO; DE MARCO; FERREIRA, 2009a; MARTINELLI et al., 2010).

To derive policies for reducing human impacts on native biota in the Cerrado, we need to understand whether different land practices differ in their impacts and whether different mechanisms for protection are needed to protect different natural habitats (CARVALHO; DE MARCO; FERREIRA, 2009a). Previous studies in small portions of the Cerrado found different impacts of crops and pastures on Cerrado habitat loss. In the northeast of the biome, in the new frontier of agricultural expansion, there was no difference in habitat loss in landscapes dominated by crops or pasture (ASSIS; ESCADA; AMARAL, 2021). In the central part of the biome, in the old colonization portion, landscapes dominated by crops lost more habitat than landscapes dominated by pastures (CARVALHO; DE MARCO; FERREIRA, 2009a). To the best of our knowledge, there has never been an assessment of the impacts of crops and pasture on the amount and pattern of natural habitat cover over the whole Cerrado biome.

There are currently two national policies for the conservation of natural habitats in Brazil, the National System of Nature Conservation Units (SNUC) and the

Brazilian Forest Code. Neither of these is specific to the natural habitats of the Cerrado. The SNUC creates and manages two general types of Protected Areas. The first type is entirely dedicated to nature conservation, while in the second type sustainable use of natural resources is allowed (Law nº 9.985, de 2000 July 18th). The other national policy for the conservation of natural habitats in Brazil is the Brazilian Forest Code (Law nº. 12,651 of 2012), which establishes: (1) Permanent Protection Areas, which are riparian strips of habitat along natural watercourses, lakes, and lagoons, the lands surrounding headwaters, slopes greater than 45o, restingas (vegetation of coastal sandy soils), mangroves, the edges of the tablelands or plateaus, the tops of hills, and lands higher than 1800m; and (2) Legal Reserves, which define a region-specific percentage of each public or private property that should be preserved for natural habitat. For the Cerrado, Legal Reserves assign different percentages depending on the region. If the Cerrado area is within the Legal Amazonia limits, 35% of the property should be protected. If it is outside the Legal Amazonia, 20% of the property should be protected.

These national policies for the conservation of natural habitats in Brazil do not specify protection for the different Cerrado habitat types, i.e. forest, savanna, and grassland. The Protected Areas protect around 6.5% of the remaining Cerrado natural habitats (FRANÇOSO et al., 2015), and the Legal Reserves do not specify the type of habitats that should make up the mandated protected percentage of each property. In addition, Polizel et al. (2021) stated that enforcement has been lax. Further threatening Cerrado natural habitats, a proposed law in the Brazilian Senate aims to revoke Legal Reserves “to enable economic exploitation of the areas” (Projeto de Lei n° 2362, 2019). The discussion about the effectiveness of policies for the conservation of natural habitats in Brazil for protecting Cerrado natural habitats raises the question, to what extent are these policies protecting each of the Cerrado formations – forest, savanna, and grasslands?

Beyond protecting the Cerrado from habitat loss, another important issue is the spatial pattern or configuration of the remaining natural habitat. A given total area of natural habitat can occur in a few large patches or many small patches (fragmentation per se). In a human-dominated region such as the Cerrado, many of the remaining natural patches are small. Empirical evidence suggests neutral or positive effects of fragmentation per se on species occurrence and abundance (FAHRIG, 2017) and the number of species (FAHRIG, 2020; MARTINELLI et al., 2010). This suggests that small patches are particularly important to conservation plans in fragmented landscapes. Because of this, it is important to understand the pattern of habitat that results from human activities in the landscape, to improve landscape management for conservation.

Here we investigate whether conservation of the Cerrado natural habitats differs between Cerrado landscapes dominated by pasture and those dominated by cropland. In principle, the conservation policies should apply equally, regardless of the type of agriculture in the landscape. The Brazilian Forest Code does not specify the amount of Cerrado natural habitat to be protected as a function of the type of agriculture. The null expectation is therefore that the amount of the Cerrado natural habitat does not differ between landscapes with a predominance of crops vs. pastures.

We also investigate whether the different protection policies differentially protect the Cerrado natural habitats – forest, savanna, or grasslands. We have no a priori expectation of the relative protection of different habitat types in Protected Areas because the SNUC does not specify protection by habitat type. We expect that Permanent Protected Areas protect mostly forests because most rivers and lakes in the Cerrado have riparian forests and the majority of Permanent Protected Areas protect the lands around rivers and lakes. We also have no a priori expectation of the relative protection of different Cerrado natural habitats by Legal Reserves because the Brazilian Forest Code does not specify protection by habitat type either.

Finally, we investigate whether the level of fragmentation of Cerrado's natural habitat differs in landscapes dominated by pasture vs. those dominated by cropland. We expect that the fragmentation per se of Cerrado's natural habitat is higher in a landscape with a predominance of pasture than in a landscape with a predominance of the annual and perennial crops. We base this hypothesis on the fact that agricultural mechanization results in large crop fields (MARTINELLI et al., 2010).

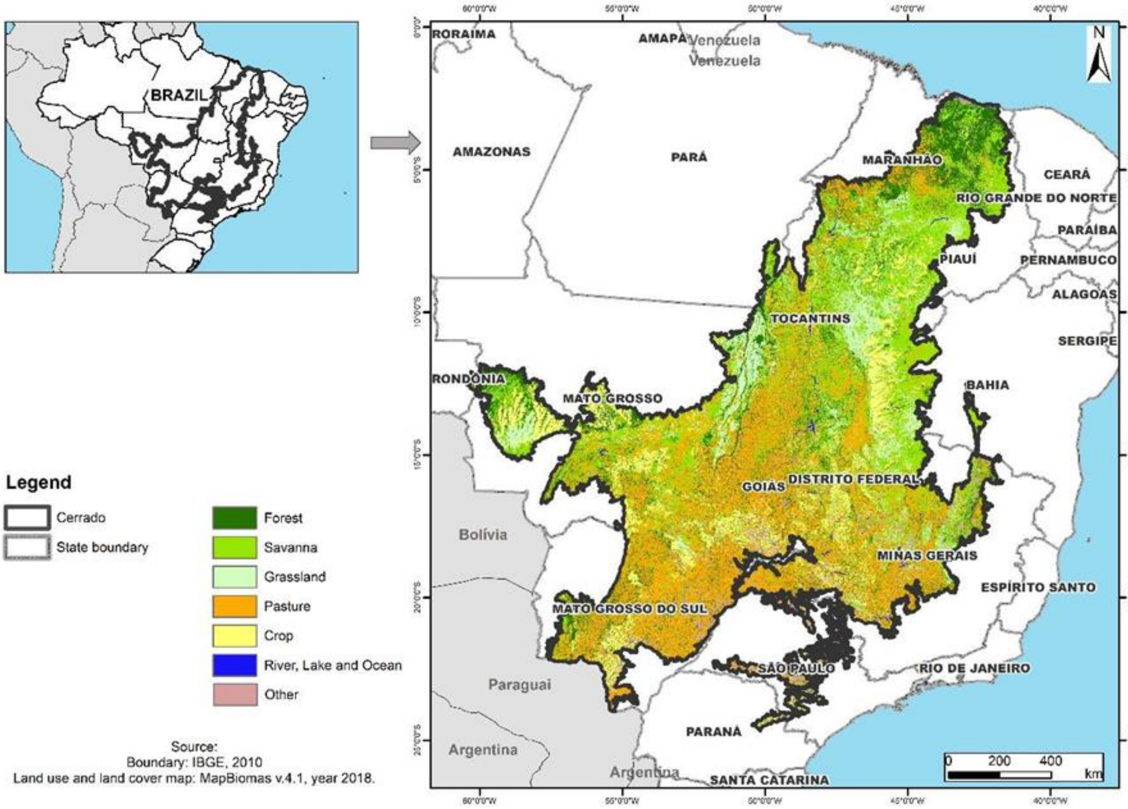
Thus, we address the following questions: (i) Does the amount of Cerrado natural habitat differ in landscapes with a predominance of pasture vs. a predominance of crops? (ii) Are the different types of Cerrado natural habitats - forest, savanna, and grassland - equally protected by the different policies for habitat protection in Brazil? (iii) Is the level of fragmentation of Cerrado natural habitat higher in landscapes with a predominance of pasture than in landscapes dominated by crops?

4.2 Material and methods

4.2.1 The Cerrado

The Cerrado biome, located mostly in the Southeast and Midwest of Brazil, occupies approximately 2 million km², or a fifth of the country (Figure 4.1). In 2018, the cropped area in the Cerrado was 250,505 km², the pasture area was 609,761 km², and the native coverage was 1,056,782 km² (SOUZA et al., 2020). The mean annual temperature is 22 - 23ºC and the average annual precipitation range is 1,200 - 1,800 mm. The Cerrado has a seasonal tropical climate with dry winters. During the dry season, it is common that vegetation loses its leaves, accumulating dry biomass on the soil. This accumulation of biomass benefits the spread of fire, which is part of the natural dynamics of the Cerrado biome (FAHRIG, 2017).

Figure 4.1. Land use and land cover of the Cerrado biome based on MapBiomas v.4.1 2018.



Source: The author.

4.2.2 Does the amount of Cerrado natural habitat differ in landscapes with a predominance of pasture vs. those with a predominance of cropland?

To answer our first question, we divided the Cerrado into a grid of 5 km x 5 km landscapes. This was a practical landscape size for computation and for ensuring variation in landscape structure across landscapes. We classified the landscapes using the land use and land cover map from MapBiomas collection 4.1, using data from 2018 (SOUZA et al., 2020), which has an accuracy of 83.8%. We used the classes of MapBiomas to identify the percentage of each class within each landscape. We considered the predominant class in the landscape to be the class with the highest area percentage. For our first question, we selected only landscapes having a predominance of crops and pasture, and we quantified the amount of Cerrado natural habitat as the sum of the classes Forest Formation, Savanna Formation, and Grassland from MapBiomas. The class crop is equivalent to Agriculture in MapBiomas, which includes both annual and perennial crops. We then determined whether the amount of Cerrado natural habitat differed between landscapes dominated by pastures vs. crops using the Wilcoxon Test.

4.2.3 Are the different types of Cerrado natural habitats - forest, savanna, and grassland - equally protected by the different policies for habitat protection in Brazil?

To answer our second question, we quantified the amount of each Cerrado natural habitat – forest, savanna, and grassland - contained within reserves resulting from each of the policies for habitat protection. We delineated the reserves using official data of Protected Areas, Permanent Protected Areas, and Legal Reserves (Brasil, Ministério da Agricultura, 2019; Brasil, 2019). We determined the percentage of each habitat type protected in each type of reserve in two ways: (i) as the percentage of the original area (before any land conversion) of each Cerrado natural habitat (IBGE, 2004) that is now protected by each type of reserve; and (ii) as the percentage of the current area (estimated in 2018) of each Cerrado natural habitat that is under protection by each type of reserve. This data source categorizes 28 native plant communities in the Cerrado from IBGE, which we clustered into the 3 main habitats - forest, savanna, and grassland - following Brito (2016). We verified the total amount of Cerrado natural habitat inside each type of reserve.

4.2.4 Is the level of fragmentation of the Cerrado natural habitat higher in landscapes with a predominance of pasture than in landscapes dominated by crops?

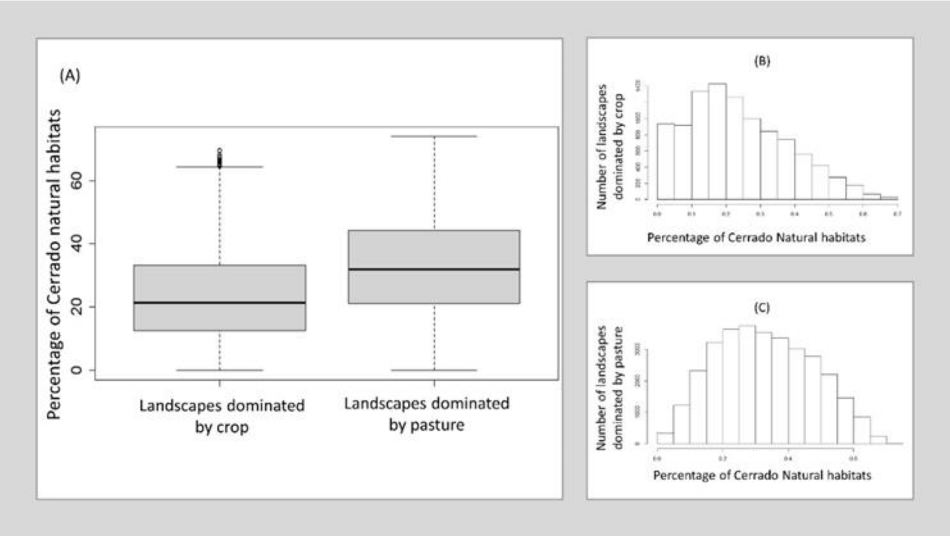
To answer our third question, we selected landscapes classified as predominantly pasture or predominantly crops (see Question 1), containing the same range in the amount of natural habitat. We controlled for the amount of natural habitat because we were measuring fragmentation per se, i.e. number of patches independent of the amount of habitat (FAHRIG, 2017). We used histograms to find the range with the highest frequency of landscapes - between 20% and 30% of natural habitats - to maximize our sample size.

We used as fragmentation metrics the Total Edge and Number of Patches of the Cerrado natural habitat, following FAHRIG (2017). We obtained the Total Edge for each landscape using the sum of the perimeter of all patches of the Cerrado natural habitat and the Number of Patches as the sum of all patches of the Cerrado natural habitat in a landscape. The patches that crossed the borders between landscapes were included in the analysis of both landscapes, attributing the total value of the patch area for both landscapes. Landscapes crossing the boundary of the Cerrado region were excluded from the analysis. We then compared the Total Edge and Number of Patches of the Cerrado natural habitat in landscapes classified as pasture to those classified as crops (from Question 1) to test if they differ using the Wilcoxon Test.

4.3 Results

For Question 1, contrary to our expectation, we found more Cerrado natural habitat areas in landscapes with a predominance of pasture than in landscapes with a predominance of crops (Figure 4.2). On average, the landscapes with a predominance of crops contained 23.5 % natural habitat, and those with a predominance of pasture contained 32.9 % natural habitat.

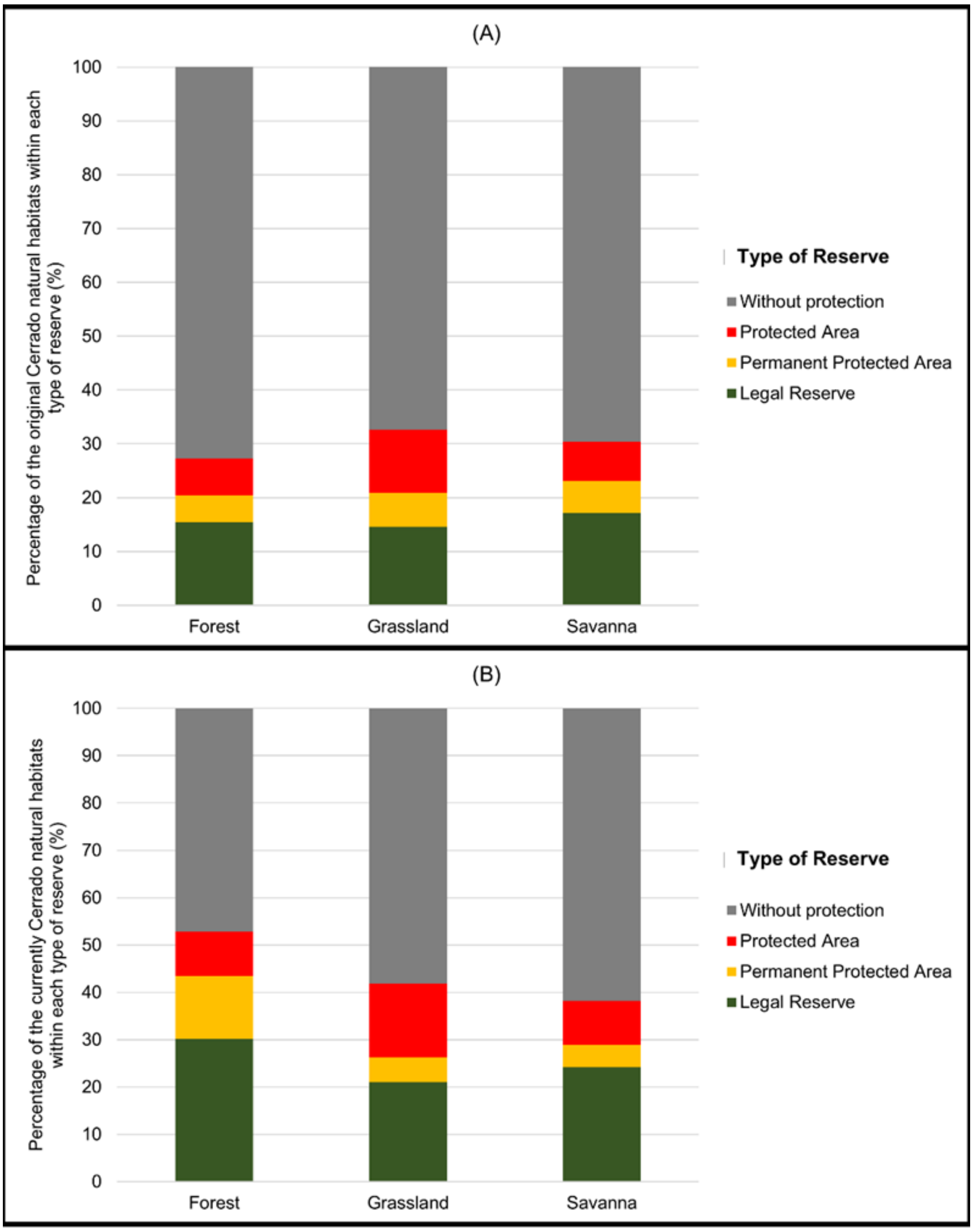
Figure 4.2. The percentage of Cerrado natural habitat is higher in landscapes with a predominance of pasture than in landscapes with a predominance of crops (W = 1.04 x 109, p-value = 2.2 x 10-16) (A). Most landscapes dominated by crops have less than 30% natural habitat (B). Most landscapes dominated by pasture have between 20% and 40% natural habitat (C).



Source: The author.

For Question 2, contrary to our prediction, we found that the percentage of the original area that is currently protected is similar for the three different types of Cerrado natural habitats, with about 30% protected for each (Appendix A.1, Figure 3). However, different types of reserves protect different amounts of the three habitat types. Legal Reserves protect the largest proportion of all the Cerrado natural habitats – forest (15%), savanna (17%), and grassland (15%). Protected Areas protect more grassland (12%) than forest (7%) and savanna (7%). Permanent Protection Areas protect the smallest proportions – forest (5%), savanna (6%), and grassland (6%).

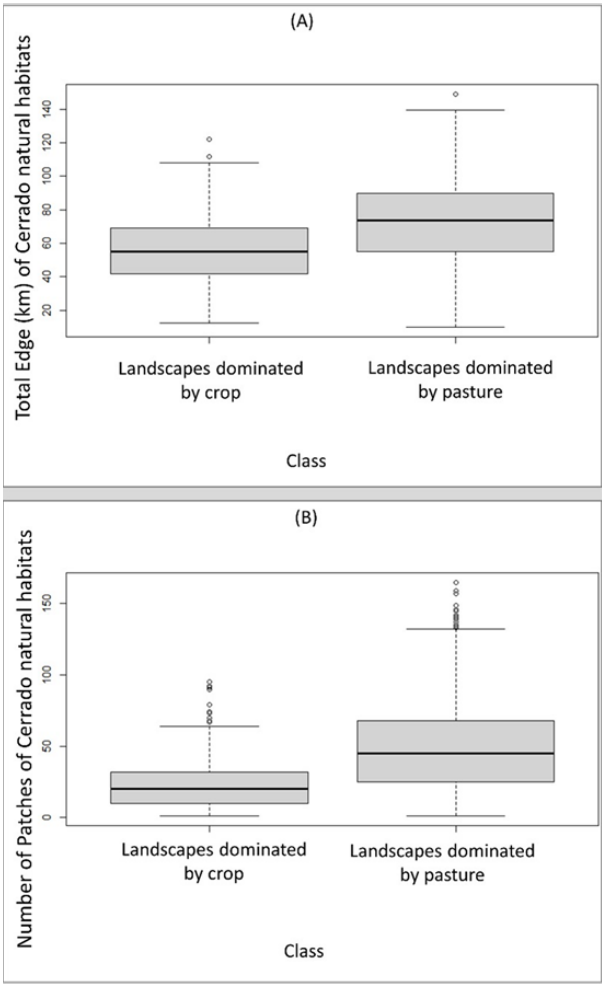
Figure 4.3. The percentages of the original (A) and current (B) distributions of the Cerrado natural habitats - forest, savanna, and grasslands - under protection in the three Brazilian types of reserves. Overall, the three Cerrado natural habitats are about equally protected relative to their original amounts, with about 30% of the original area of each protected (A). Relative to their current amounts, a larger proportion of forests are under protection than other Cerrado natural habitats.



Source: The author.

Finally, for Question 3, as predicted, we found that the fragmentation per se of the Cerrado's natural habitat is higher in landscapes with a predominance of pasture than in landscapes with a predominance of crops. This is the case whether fragmentation is measured as Total Edge or as the Number of Patches of Cerrado's natural habitat (Appendix A.1, Appendix A.2, Figure 4).

Figure 4.4. Cerrado natural habitats in landscapes with a predominance of crops are less fragmented than in landscapes with a predominance of pasture. (A) The Total Edge of natural habitat in landscapes with a predominance of crops is smaller than the Total Edge of natural habitat in landscapes with a predominance of pasture (W = 1.09 x 107, p-value < 2.2e-16). (B) The Number of Patches of the Cerrado natural habitat in landscapes with the predominance of crops is smaller than the Number of Patches of the Cerrado natural habitat in landscapes with the predominance of pasture (W = 8.05; x 106, p-value < 2.2e-16).



Source: The author.

4.4 Discussion

We found that the loss of Cerrado's natural habitat is higher in landscapes dominated by crops than those dominated by pastures. This is not expected, a priori, because habitat protection policies in Brazil do not differ for these two major types of agriculture. Our results are similar to those found in previous studies focused only on the northern part of the Cerrado biome, where the highest rates of Cerrado natural habitat loss are located (ASSIS; ESCADA; AMARAL, 2021; POLIZEL et al., 2021). Our result is consistent with the observation that in the past decade crops have shown the largest expansion at the expense of Cerrado's natural habitat (SOUZA et al., 2020).

On the other hand, our results suggest there is little or no bias in the type of Cerrado´s natural habitat being protected by current habitat conservation policies. The national policies for the conservation of natural habitats in Brazil protect about the same total proportions of the original cover of the three main Cerrado natural habitats - grassland, savanna, and forest. We had expected more forests to be protected because of the criteria for Permanent Protected Areas which specify the protection of forested riparian areas. However, this may be balanced by the presence of more grassland and savanna in other categories of Permanent Protected Areas, such as slopes greater than 45o, the tops of hills, and lands higher than 1800m. Although neither the SNUC nor the Brazilian Forest Code specifies the amount of each type of Cerrado natural habitat to be protected, the three types are almost equally distributed among them. We suggest that future conservation policies should explicitly continue to ensure the conservation of every natural habitat type in the Cerrado.

As a proportion of the current cover of the Cerrado natural habitats, there is a larger proportion of current forest than savanna or grassland under protection. Since 1985, about 23% of forest, 18% of savanna, and 8% of grassland have been lost (ALENCAR et al., 2020). The fact that forests showed the largest loss explains why we find a larger proportion of current forest in reserves: the proportion of forest in reserves increases as forest outside reserves is lost. This result reinforces the need for conservation policies going forward to ensure the conservation of natural habitats in proportion to their original relative covers. In particular, relying on the current cover would lead to an under-representation of protected forests.

Considering both the low percentage of Cerrado natural habitats currently in Protected Areas and Permanent Protected Areas, revoking Legal Reserves as proposed by the Brazilian Senate would greatly increase the susceptibility of the Cerrado biome to the loss of its native areas. Among the mechanisms of conservation, Legal Reserves protect the highest proportion of the Cerrado natural habitats. Besides, Legal Reserves can work to improve connections among Protected Areas because in principle they are distributed across all properties over the whole biome. If effectively implemented, this would increase connectivity among natural areas in both private and public lands (ROSA, 2021, p. 20). (ROSA, 2021) showed that Legal Reserves house threatened species, and even with a low sample size, the author registered 38% of mammal species from Cerrado inside Legal Reserves. It is also important to highlight that Legal Reserves are also an efficient mechanism for keeping biodiversity in private lands (ROSA, 2021).

Our analysis of habitat fragmentation per se relating to the type of agriculture suggests that crops have likely a larger impact on Cerrado biodiversity than pastures. For a given amount of natural habitat, the habitat in landscapes with a predominance of pasture is more fragmented than in landscapes with a predominance of crops. This pattern can be explained by the fact that the crops in Cerrado are mostly mechanized, which results in large, continuous cropped areas (MARTINELLI et al., 2010; SOUZA et al., 2020). We infer that this suggests a stronger negative impact on biodiversity in crop-dominated landscapes than in pasture-dominated landscapes because responses of species and biodiversity to fragmentation per se are mostly positive when they do occur (FAHRIG, 2017, 2020). In the Cerrado, enlargement of crop fields is concentrating the remaining Cerrado natural habitats into a small number of relatively large patches.

Our results show that by both reducing the habitat amount and reducing fragmentation per se of natural habitats crops have a bigger impact on biodiversity conservation in the Cerrado than pasture. Our results appear to be different from CARVALHO et al. (2009) who reported higher fragmentation in landscapes with a dominance of crops than in landscapes with a dominance of pastures in central Cerrado. They calculated landscape metrics - number of patches, total area, edge density, patch area, shape index, and mean Euclidean nearest neighbor distance - in cells dominated by crops or pasture. The difference between their results and ours may be associated with the fact that CARVALHO et al. (2009) did not consider fragmentation per se in their study and so the effect of fragmentation in their study is probably combined with (and dominated by) the effect of habitat amount. Overall, our results highlight the conservation value of small natural patches to conservation in pasture-dominated landscapes.

4.5 Conclusion

Our findings have three main implications for conservation in the Cerrado. First, our result showing that Legal Reserves preserve more Cerrado natural habitat than other reserve types demonstrate that revoking Legal Reserves, as has been proposed by the Brazilian Senate, would render the Cerrado region much more susceptible to the loss of its natural habitats. Second, public policies should be designed primarily for the conservation of the Cerrado natural habitats within the crop-dominated landscapes, because natural habitats are most at risk in those landscapes. And, finally, environmental policies should be proposed to encourage the regeneration and maintenance of small patches of natural vegetation in the crop-dominated landscapes of the Cerrado region.

5 SCALE AND REPRESENTATION OF LANDSCAPES IN MAMMAL STUDIES IN BRAZIL[2]

5.1 Introduction

The concept of scale refers to the ratio between a representation of distance or time measurements and their actual measurements in the real world. This definition comes from the field of geography and refers to any measurements of spatial, temporal, quantitative, or analytical dimensions used to measure and study a given phenomenon (TURNER, 1989). In this study we only discuss the spatial dimension of scale.

Spatial scales are characterized by two attributes: resolution and extent. Resolution refers to the smallest intervals in an observational set, i.e., the precision of the measure, and relates to the proportion between the represented and real dimensions (GIBSON; OSTROM; AHN, 2000, p. 20; TURNER, 1989, p. 198). This implies that a given resolution is dependent on a given source or data or mapping. For example, in a map withs a spatial resolution of 30 m from its data source, only targets larger than 30 x 30 m would be discriminated. Extent refers to the spatial range that observations at a particular resolution are made and provides the total area to be considered as a landscape in the study (GIBSON; OSTROM; AHN, 2000, p. 20).

Landscape Ecology studies examine the ecological interactions that occur in heterogeneous landscapes and usually contemplate two analytical stages. The first stage summarizes the population or community structures, and the second stage relates them to environmental variables (DRAY et al., 2012). There is empirical and theoretical evidence indicating that both resolution and extent impact how the relationship between species traits and environmental predictions are measured (SUÁREZ-CASTRO et al., 2018). Therefore, when

---

[2] Based on: ASSIS, T. O.; CÁCERES, N. C.; PASSAMANI, M.; AMARAL, S. Scale and representation of landscapes in mammal studies in Brazil. Acta Oecologica, v. 114, n. January, 2022.

collecting environmental variables, it is essential to choose both the best resolution to represent them and the extent to which they will be evaluated. Given that it is not possible to observe something smaller than the detail of its resolution (FORMAN, 1995), the resolution of a landscape representation must be such that it allows the target processes of the study to be observed (ALLEN; HOEKSTRA, 1990). Additionally, the extent must be compatible with the scale of effect, i.e., the scale at which the response variable best responds to the predicted variable (JACKSON; FAHRIG, 2012).

The relationship between response variables and predicted variables is dependent on the scale used to evaluate them (MARTIN, 2018). Species attributes, such as fecundity, abundance, and occurrence, should differ when evaluated on the same scale (MORAGA; MARTIN; FAHRIG, 2019). Similarly, different predictor variables have different scales of effect for the same species (JACKSON; FAHRIG, 2015). Although the chosen scale of effect is often based on species parameters, such as home range, dispersal, and body size, this relationship is not always direct (JACKSON; FAHRIG, 2012). Area and distance measurements associated with biological parameters, such as dispersion and home range, should not be used as scale of effect values, however, these parameters are essential to establishing useful intervals to evaluate possible scales in an effort to find the appropriate scale of effect (JACKSON; FAHRIG, 2012, 2015).

Once the best scale has been chosen, the next step is to choose how to best represent the landscape space. To that end, the response variable to be measured for the species in question must be considered, along with which the landscape structures used by the species. In this study we consider representation to be the choices concerning landscape heterogeneity, including the structures and land cover types. Three types of structures exist in a given landscape mosaic: patch, corridor, and matrix. A patch is a non-linear homogeneous area that differs from its neighborhood. Corridors are straight portions of vegetation surrounded by a different type of land-cover (matrix), usually connecting patches. Finally, a matrix is a predominant land cover area in the landscape which, therefore, controls the dynamic inside the landscape (FORMAN, 1995).

Determining the best scale means choosing the appropriate spatial resolution, scale of effect, and representation. To discuss how best to choose the spatial-scale and landscape representation, we carried out a review of landscape scale studies targeting mammals in Brazil and evaluated their approach to the scale issue. We chose Brazil as the spatial extent because it comprises six different biomes and, therefore, represents a heterogeneous environment in this discussion. Moreover, we chose mammals as the target group because of their differences in size, dispersal, and home ranges, therefore providing the opportunity to include an element of heterogeneity in the analysis.

In this context, we seek to answer the following questions: how do mammal focused landscape-scale studies in Brazil deal with scale? Is there a common approach among mammalian landscape ecology studies in Brazil to define the scale and representation of landscapes? To answer these questions, we carried out a review of mammals and landscape ecology studies in Brazil to, first, survey how previous research has addressed scale and landscape representation and, second,to discuss the best practices and directions to follow based on Landscape Ecology concepts. This study is structured as follows: first, we introduce how landscape ecology studies in Brazil have approached the scale issue, then, we use the concepts of landscape ecology and the knowledge about how mammals perceive and use their environments to address the relevance of scale and how it affects the study of mammals.

5.2 Material and methods

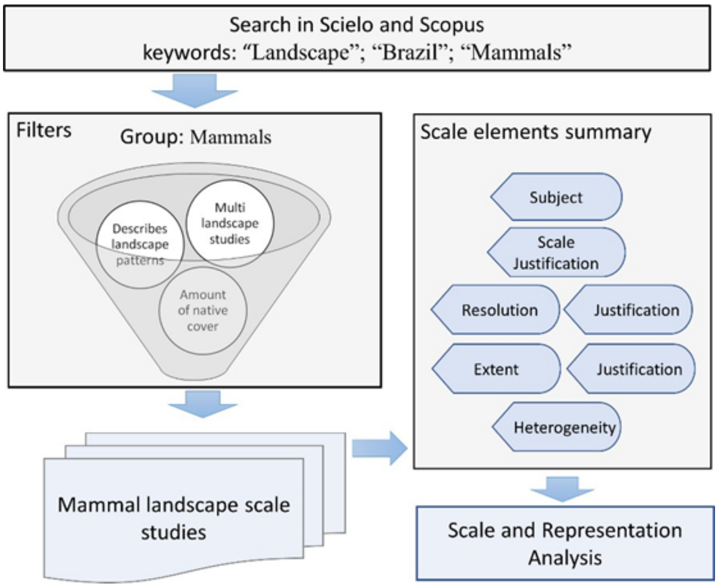
Although the landscape scale and representation discussion are relevant everywhere, we restrict our analysis to Brazil. Our study area covers 8.516.000 km², comprised six biomes (Amazon, Caatinga, Cerrado, Atlantic Forest, and Pampa), and includes several different environments. We also restricted the biological group to mammal, given that they make up a group of animals with different body sizes, and different ranges of movement across the landscape. We also limited our scope of analysis to scientific studies carried out at the landscape scale.

To understand how studies on the Landscape Ecology of mammals in Brazil address landscape scale and representation, we carried out a literature review of papers published in specialized journals. Specifically, we searched the online scientific publication databases Scopus and Scielo (Scientific Electronic Library Online) for papers published up to November 2019. We did set any search restrictions on the earliest published date. The Scopus library is updated daily and consists of a collection of more than 21,000 articles. Scielo, in turn, is a Brazilian electronic library and consists of a selected collection of Brazilian scientific journals. These libraries are important indexing sources for scientific publications in Brazil. Our search strategy consisted of selecting all articles that contained the following words in title, abstract, or keywords: landscape, Brazil, and mammals. Once we had narrowed down our search, we analyzed all papers to evaluate whether their research had been carried out at the landscape scale.

We adopted the following definition of landscape: a heterogeneous land area composed of a cluster of interacting ecosystems that are repeated in similar form throughout (FORMAN; GODRON, 2008). Based on this definition, we considered landscape scale papers to be those that met the following criteria: (1) multi landscape studies, i.e., studies that encompass more than one landscape and describe the limits of the landscape analyzed, thereby making it possible to compare results among them; (2) studies that describe landscape patterns by presenting the landscape structures analyzed and the characteristics of those structures; and (3) studies that quantify the amount of native vegetation cover in the landscapes studied.

From our narrowed down search papers that considered the landscape scale, we then excluded all papers that did not use mammals as their main biological group of analysis. Next, we searched for the author justifications of why they had used the chosen scale, both in their spatial (resolution and extent), and temporal components (resolution and extent). We also investigated which type of landscape representation the authors had adopted. We synthesized the results with the following information for each paper reviewed: (1) whether the author(s) had justified their choice of scale or not; (2) the resolution size chosen; (3) the justification for choosing the resolution size used; (4) the extent chosen; (5) the justification used for choosing the extent used; (6) matrix heterogeneity; and finally, (7) the topic of the paper. When the resolution was not explicitly cited in the text, but the article cited a remote sensing image used to classify the land use and coverage, we used the image’s spatial resolution and swath references to infer the resolution (Figure 5.1).

Figure 5.1. Method used to select papers for review. First, we searched for the keywords in the scientific publication databases Scielo and Scopus. Second, we narrowed down the selection to only the papers that targeted mammals as the biological group. Third, we further narrowed down our selection to only the papers that had used the landscape scale. Finally, we extracted scale and heterogeneity information from all papers.



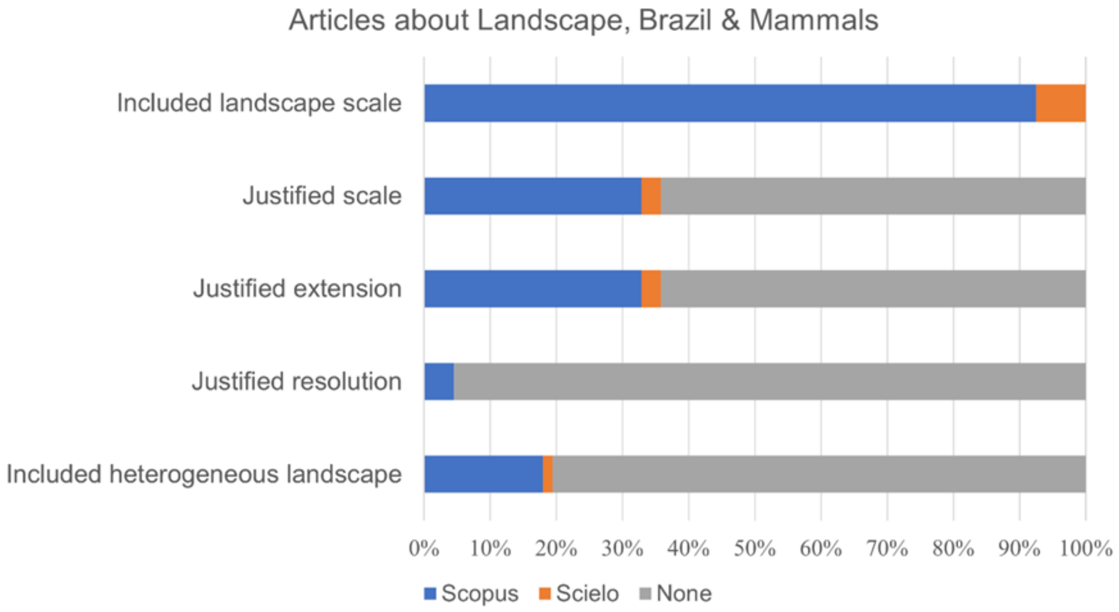
Source: The author.

The information described in the scale elements summary (Fig 1) was considered as attributes to describe how scale choices are usually made. We compiled the scale choice justifications from all papers and counted them. Next, we searched how the matrix heterogeneity was considered in each paper. Specifically, we took note of whether the paper had adopted a binary matrix, characterized by a forest/non-forest landscape, or a heterogeneously quantified landscape with other land use land cover classes. We also indexed the subject of each paper to relate them to the choices of landscape representation. Moreover, we recorded both the period of analysis informed in each paper and the time extent of each study.

5.3 Results

Our initial search resulted in a total of 161 articles from Scopus and 22 articles from Scielo. After filtering these articles according to landscape scale criteria, we reduced our sample to 62 articles (38.5%) from Scopus and 5 articles from Scielo (9.1%). Among those articles, 24 (35.8%) justified at least one component of their chosen landscape scale (Figure 5.2, Table 5.1).

Figure 5.2. Percentage of papers in search results that used the landscape scale (67) and justified both spatial scale components and heterogeneity.



Source: The author.

Table 5.1 Summary of papers accounting for each attribute evaluated. The number in parentheses represents the proportion of all papers conducted at the landscape scale.

	Considered landscape heterogeneity	**Justified resolution**	**Justified extension**	**Justified scale**	**Conducted study at the landscape scale**
Scopus	12 (17.9%)	3 (4.5%)	22 (32.8%)	22 (32.8%)	62 (92.5%)
Scielo	1 (1.5%)	0 (0.0%)	2 (3.0%)	2 (3.0%)	5 (7.5%)

A total of 24 articles (22 from Scopus and 2 from Scielo) justified the choice of spatial scale. Of those24 studies, all justified the extent used, but only 3 papers, all from Scopus, justified the resolution used. We identified three methods that authors used to justify the chosen extent: (1) based only on spatial characteristics, (2) based on the relationship between species behavior and space, and (3) by testing the scale of effect (Table 5.2). The argument most frequently used to justify extent was the “scale of effect”. Moreover, justifications for choosing a given resolution included: home range, connectivity, minimal distance between traps, movement, and empirical evidence. When the authors based their scale justification on home range, movement, connectivity, and empirical evidence, the resolution was chosen to represent the structures used by their study species in the landscape. When the authors used minimal distance between traps as justification for their chosen resolution, the minimum resolution was chosen to avoid spatial correlation, i.e., to avoid counting the same trap twice in the same event.

Table 5.2 Papers discussing Landscape, Brazil, and Mammals at the landscape scale, in which authors have justified their choice of scale. Summary of the subject, biological group, space scale components (extent and resolution), and landscape representation (matrix heterogeneity) of the papers.

Reference	Group	Subject category	Spatial Scale				Matrix heterogeneity
			Extent	Extent justification	Resolution (m^2)	Resolution justification	
(PARRY; BARLOW; PERES, 2009) Allocation of hunting effort by Amazonian smallholders: Implications for conserving wildlife in mixed-use landscapes.	Mammals	Hunting	10,000 m	Extent of effect	900	No	Yes
(FREITAS et al., 2012) A model of road effect using line integrals and a test of the performance of two new road indices using the distribution of small mammals in an Atlantic Forest landscape.	Small mammals	Road ecology	50 - 1,000 m	No	400	No	Yes
(MENDES; DE MARCO, 2018)Bat species vulnerability in Cerrado: Integrating climatic suitability with sensitivity to land-use changes.	Bats	Habitat amount/ Fragmentation	9.25 km Cerrado	Landscape/ Species distribution	853.776	Movement	No
(HARDT et al., 2015) Does certification improve biodiversity conservation in Brazilian coffee farms?	*Priodontes maximus* and *Marmosops incanus*	Sustainable Agriculture Network	Micro Basin	Similarity in environmental conditions	500	Connectivity	Yes
(VIEIRA et al., 2018) Fair tests of the habitat amount hypothesis require appropriate metrics of patch isolation: An example with small mammals in the Brazilian Atlantic Forest.	Small mammals	Habitat amount	300 - 6,700 m	Scale of effect	500	No	No
(REGOLIN et al., 2017) Forest cover influences occurrence of mammalian carnivores within Brazilian Atlantic Forest.	Carnivores	Fragmentation	250 - 2,000 m	Tested	5	No	Yes
(PÜTTKER; MEYER-LUCHT; SOMMER, 2008) Fragmentation effects on population density of three rodent species in secondary Atlantic Rainforest, Brazil.	Small mammals	Fragmentation	800 m	To avoid spatial correlation	400	No	No
(MIGUEL et al., 2019) Habitat amount partially affects physiological condition and stress level in Neotropical fruit-eating bats	Bats	Habitat amount	2,000 m	Previous studies/scale of effect	1	No	No
(DELCIELLOS et al., 2018) Habitat fragmentation affects individual Condition: Evidence from small mammals of the Brazilian Atlantic Forest.	Small mammals	Habitat amount/ Fragmentation	900 m	Movement	500	No	No

Continue

Table 5.2 Continuation.

Reference	Group	Subject Category	Spatial scale				Matrix heterogeneity
			Extent	Extent justification	Resolution (m^2)	Resolution justification	
(FARIA et al., 2015) Implications of habitat loss on seed predation and early recruitment of a keystone palm in anthropogenic landscapes in the Brazilian Atlantic rainforest Leiza Aparecida S. S. Soares	Small mammals and plants	Seed predation	2,000 m	No	20	No	No
(BUENO; FAUSTINO; FREITAS, 2013) Influence of landscape characteristics on capybara road-kill on highway BR-040, Southeastern Brazil.	Capybaras	Road ecology	1,000 m	Tested	25000	No	Yes
(HENDGES et al., 2017) Landscape attributes as drivers of the geographical variation in density of *Sapajus nigritus* Kerr, 1792, a primate endemic to the Atlantic Forest	Primate	Climate changes	20,000 m	Scale of effect	900	No	Yes
(MORAES et al., 2018) Landscape resistance influences effective dispersal of endangered golden lion tamarins within the Atlantic Forest.	Primate	Landscape heterogeneity	5,000 m	Movement		No	Yes
(BERTASSONI et al., 2019) Land-use changes and the expansion of biofuel crops threaten the giant anteater in southeastern Brazil.	Giant anteater	Landscape changes	São Paulo	No	1000000	Home range	Yes
(DOTTA; VERDADE, 2011a) Medium to large-sized mammals in agricultural landscapes of south-eastern Brazil.	Medium and large mammals	Distribution	2,000 m	To avoid spatial correlation	400	No	Yes
(HANNIBAL et al., 2018a) Multi-scale approach to disentangle the small mammal composition in a fragmented landscape in central Brazil.	Small mammals	Scale of effect	1,000 m	To avoid spatial correlation / home range	900	No	No
(PALMEIRIM et al., 2018) Small mammal responses to Amazonian forest islands are modulated by their forest dependence.	Small mammals	Insularization	250 - 1,000 m	Scale of effect	25	No	No
(CARVALHO; DE MARCO; FERREIRA, 2009b) The Cerrado into-pieces: Habitat fragmentation as a function of landscape use in the savannas of central Brazil.	Endangered mammals	Fragmentation	Goiás	No	900	No	Yes
(ZIMBRES et al., 2013a) The impact of habitat fragmentation on the ecology of xenarthrans (Mammalia) in the Brazilian Cerrado.	Xenarthrans	Fragmentation	400 and 900 m	Home range	900	No	No

Continue

Table 5.2 Conclusion.

Reference	Group	Subject Category	Spatial scale				Matrix heterogeneity
			Extent	Extent justification	Resolution (m^2)	Resolution justification	
(PIMENTA et al., 2018) The return of giant otter to the Baniwa Landscape: A multi-scale approach to species recovery in the middle Içana River, Northwest Amazonia, Brazil.	Giant otter	Fishing management	250 - 1,000 m	Scale of effect	156.25	No	Yes
(MELO et al., 2017b) Testing the habitat amount hypothesis for South American small mammals.	Small mammals	Habitat amount	250 and 600 m	Scale of effect	900	No	No
(ROCHA et al., 2018) Effects of habitat fragmentation on the persistence of medium and large mammal species in the Brazilian Savanna of Goiás State.	Medium and large mammals	Extinction debt	2,000 m	Scale of effect/To avoid spatial correlation	No	No	No

In most of the selected articles, their representations considered the heterogeneity of the landscape. Overall, 13 papers (12 from Scopus and 1 from Scielo) considered the landscape matrix to be a heterogeneous environment in their studies. It is not possible to identify a common scientific interest among these papers. The main subject of each article varied from hunting to road ecology, fragmentation, scale of effect, climate change, and landscape changes, among others, as shown in Table 3.2. Among the articles that simplified the landscape matrix heterogeneity by representing it by as a binary representation composed of forest/non-forest areas, habitat amount and fragmentation were the predominant subjects, corresponding to 66.7% of all landscape matrix heterogeneity articles.

5.4 Discussion

Similar to the findings of Jackson and Fahrig (2015), we observed that the majority of studies on landscapes and mammals in Brazil do not justify the reasons for their choices of scale and landscape representation. This can lead to misinterpretations and omissions about events such as movement or habitat that are not noticeable in the chosen scale.

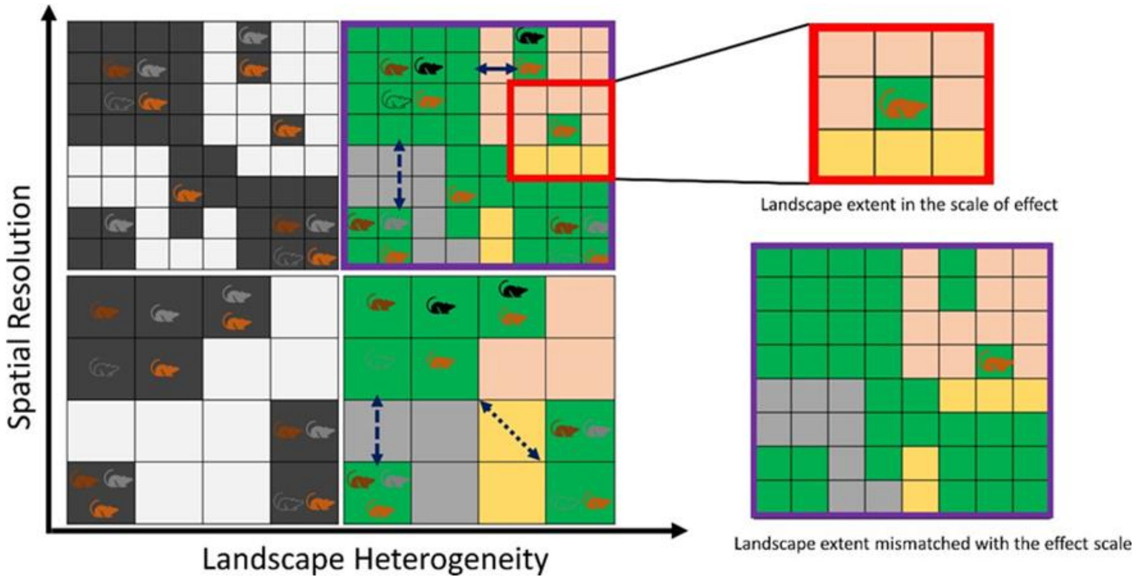
Among the studies carried out in Brazil that we analyzed, we identified three ways that the authors used to justify their choice of spatial scale extent: (1) based solely on spatial characteristics, such as distance, to avoid spatial correlation among sample units (DOTTA; VERDADE, 2011b; HANNIBAL et al., 2018b; PÜTTKER et al., 2008); (2) based on the relationship between species behavior and space, such as dispersal or daily movement (DELCIELLOS et al., 2018; MORAES et al., 2018) and home range (ZIMBRES et al., 2013b); and (3) to test the scale of effect and experiment with different extent sizes to find the scale that the species best answers to the landscape (BUENO; FAUSTINO; FREITAS, 2013; HENDGES et al., 2017; LYRA-JORGE et al., 2010; MIGUEL et al., 2019; PALMEIRIM et al., 2018, 2018, 2018; PARRY; BARLOW; PERES, 2009; PIMENTA et al., 2018; VIEIRA et al., 2018). Spatially relevant aspects of biological communities, such as home range and dispersal movement, can guide the dimension to test the scale of effect. However, Jackson and Fahrig (2012; 2015) found that when only values of dispersion or home range are used, the scale of the effect is not precisely accounted. The scale of effect can be 4 to 9 times the mean distance of dispersion and 30% to 50% of the maximum dispersion value (JACKSON; FAHRIG, 2012).

We compared studies on the same biological group that were carried out in the same biome, but which used different approaches to justify their choice of scale. Among them, for example, there were studies on small mammals in the Atlantic Rainforest. In these studies, when the argument to justify the choice of scale was to avoid spatial correlation or species movement, the extent range used was a radius of between 800 (PÜTTKER et al., 2008) and 900 meters (DELCIELLOS et al., 2018) from the sampled area, equivalent to 200 ha and 254 ha, respectively. When the authors tested the scale of effect, the radius from which species answered to the landscape was 2 km, an area equivalent to 1,256 ha (VIEIRA et al., 2018). However, when the chosen extent of analysis was not justified, this radius could reach 10,000 ha (PARDINI et al., 2010). Thus, this demonstrates that when authors do not justify their choice of scale, the extent can reach almost ten times the group's observed scale of effect (Table 5.1). In the latter study, it was not possible to link the results of richness and abundance of small mammals to the patterns described in the landscape as it was not possible to determine whether the landscape in the scale of effect preserves the same characteristics that were described for the whole area.

Once we had considered the extent, the next aspect we considered in the spatial scale was resolution. Boyce et al. (2017) found that the best scale to analyze a species-area relationship is usually the finest one, and further argue that resolution can have an impact on the aggregation of structures in a given landscape. Only three studies in our review justified their choice of resolution, all of which related this choice to species behavior, specifically movement (HARDT et al., 2015; MENDES; DE MARCO, 2018) or home range (BERTASSONI et al., 2019). Mendes and De Marco (2018) used movement to justify their choice of resolution for bats and found a resolution of 853.776 m2. Hardt et al. (2015) used connectivity to justify their choice of resolution in a study of Priodontes maximus and Marmosops incanus and found a resolution of 500m2 (HARDT et al., 2015). Finally, Bertassoni et al. (2019) used home range to justify their choice of resolution in a study of giant anteaters and found a resolution of 1,000,000 m2. These papers all indicated that their choice of resolution was enough to represent structures in the landscape that species need for their home range and movement.

It is reasonable to consider that the choice of resolution also depends on available resources and data sources. However, this choice can impact study results. Given that most of the papers discussed here did not justify or describe their choice of resolution, it is not possible to evaluate whether the resolution was enough to support their conclusions. This is particularly impactful when the subject is related to connectivity or habitat amount in the landscape because an inadequate resolution can omit structures in the landscape. When it comes to examining connectivity, it is fundamental that the structures used by the species in question, such as habitat or movement, be represented (SOZIO; MORTELLITI, 2016). The spatial resolution must be enough to represent those elements of structure. If the resolution is higher than the size of the corridors, for example, the landscape will appear less connected than it is. In other words, the scale will omit structures that work as connections in the landscape. In such cases, the effect of the corridors on the community is not possible to measure and, thus, will end up being underestimated (Figure 5.3). The same logic applies to quantifying habitat amounts, as the chosen resolution can omit small patches and corridors that serve as habitats for the species.

Figure 5.3. Effects of landscape scale and choices to represent landscape processes. As spatial resolution (pixels size) increases, landscape flows (blue arrows) become better represented among the studied group (different species of small mammals represented by different mice colors). The slash arrows' width represents the intensity of the flows: continuous arrows represent more intense flows. When landscape heterogeneity (represented by different pixel colors for different land use and land cover) is considered, more interactions and spatial relationships, e.g., border and connectivity effects, become evident. Here we can observe that the choice of a small resolution (upper quadrant) allows us to see structures in the landscape that are omitted with the choice of a bigger resolution (lower quadrants). The same applies to the choice of heterogeneity: the binary representations (left) omit different types of matrices (right) that offer the species different degrees of permeability. Landscape metrics are different in different spatial extents (purple square and red square).



Source: The author.

After considering the scale extent and resolution, we looked at landscape heterogeneity. We observed in the results section that this characteristic is more frequently discussed in landscape ecology studies (Table 5.1). Overall, we found that the choice to represent the landscape as either heterogeneous or a forested/non-forested environment was related to the guiding research questions. Fragmentation and habitat amount were found to be the main elements in the studies to represent the landscape as forested/non-forested. This can be associated with the fact that it is easier to obtain metrics in a binary matrix whereas a complex matrix would demand more metrics to describe habitat amount and fragmentation. Additionally, many studies considered a specific community in their analysis, meaning that the concept of habitat may vary according to the species being studied. Even though accounting for the unique features of the species in question to represent habitat makes the model more realistic, simplifying to a binary representation makes the model more general and makes it possible to apply to more species. Nevertheless, some fragmentation and habitat studies represent the landscape as a heterogeneous environment (Table 5.1). CARVALHO et al. (2009), for example, reported the effects of considering different land uses on the amount of habitat for mammal species in the Brazilian Cerrado. In this case, the heterogeneous environment perspective not only brought the effect of habitat amount to species but also the effect of the landscape changes to the analysis.

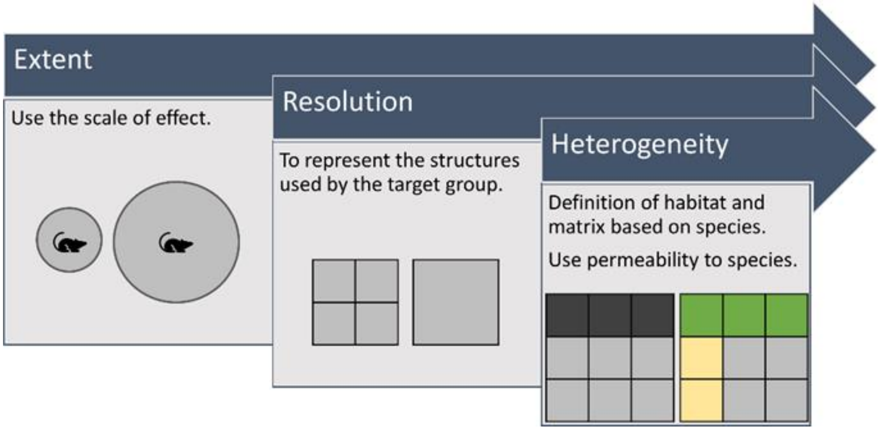
To understand the environment from the perspective of any particular species, distinct classes of anthropic cover could have different effects on the species, not only acting as a definitive barrier to the movement of organisms (UMETSU; PAUL METZGER; PARDINI, 2008). Thus, different species can use the anthropic coverings in a heterogeneous landscape to a greater or lesser extent (PREVEDELLO; VIEIRA, 2010b). Thus, a binary representation of a landscape, such as forested/non-forested, can hide different levels of fluxes that can occur in the matrix. This also can happen for a native cover. For example, the Brazilian Cerrado has at least three main distinct environments: forest, savanna, and grasslands. Each of these environments is home to species of small mammals, and their occurrence is related to these environments (ALHO; PEREIRA; PAULA, 1986). The choice of representing all of these environments as unique native covers would lead to wrong conclusions about habitat amounts.

Finally, we recommend three steps to choose the best scale and representation. First, choose the extent based on the scale of effect. Second, choose the resolution based on the structures in the landscape that are used by the mammal group. Last, choose heterogeneity according to the species' perception of the environment (Table 5.3 and Figure 5.4).

Table 5.3. Recommendations to define scale attributes according to landscape concepts.

Scale components	Recommendations
Extent	The extent must be large enough to encompass the scale of effect. It should be specific to the group being studied and the landscape considered.
Resolution	The smallest unit for spatial observation must be compatible with the dimensions of the structures (patch, corridor, matrix) used by the target group.
Heterogeneity	The landscape heterogeneity must include the different landscape environments that influence the permeability of species movement.

Figure 5.4. Process to follow when choosing a scale in landscape studies. The first step is to choose the resolution, considering the one best able to represent the landscape structures used by the target biological group. The second step is to consider the extent of the landscape, given by the scale of effect. Finally, the landscape heterogeneity should be enough to represent the habitat dimension for different species and differences in landscape permeability to species.



Source: The author.

5.5 Conclusion

We found that there is neither a general nor specific approach to justifying the choice of scale in studies of the landscape ecology of mammals in Brazil. Surprisingly, most of the studies reviewed do not mention their choice or whether it is appropriate for their objectives. To consider the best scale to analyze the effects of landscape, it is necessary to observe the elements of the landscape that affect biological responses. The elements that affect biological responses consist of the abiotic environment, biotic environment, natural disturbances, and anthropogenic disturbances. To represent the components of the landscape the biological processes should be used as a guide to define spatial scale and representation.

Our review demonstrates that studies on landscape ecology for mammals in Brazil need to better define and describe their adopted choices of landscape scale and representation to guarantee that these choices are consistent with their research objectives. We discussed that absent or inadequate definitions of landscape scale and representation can lead to underestimated and misinterpreted results. The systematic directions presented here can serve as a guide to appropriate landscape scale and representation choices in future studies on landscape ecology.

6 IS THE MATRIX STRUCTURE A GOOD MEASURE OF MATRIX QUALITY? A STUDY CASE IN THE BRAZILIAN CERRADO NATURAL HABITATS

6.1 Introduction

Human activities are expanding, causing the conversion of natural areas to anthropogenic land covers. In tropical areas, especially in Sub-Saharan Africa

and South America, the main driver of land conversion is agricultural expansion (LAURANCE; SAYER; CASSMAN, 2014). According to the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), losses of native cover to agricultural expansion are also one of the main direct drivers of species extinction, being responsible for around 30% of the threatened species in terrestrial systems (SECRETARIAT, 2019).

Strategies to minimize the negative effects of agricultural expansion on biodiversity in human-dominated landscapes must combine the preservation of natural patches with lower-impact human activities in the human-altered areas (the landscape "matrix"). Proposed strategies include: maintaining at least a given amount of natural habitat (ARROYO-RODRÍGUEZ et al., 2020); preserving not only large but also small natural patches in the landscape (FAHRIG, 2020) establishing stepping stones (BOSCOLO et al., 2008) and corridors (PARDINI et al., 2005); and improving matrix quality by planting organic crops and by using mixed farming systems and agroforests (BOESING; NICHOLS; METZGER, 2018).

The matrix can influence the persistence of natural animal populations in human-dominated landscapes through effects associated with species movement, availability of resources, and disturbance (DRISCOLL et al., 2013). Different types of matrix cover can have different degrees of resistance to species movement related to how species perceive the matrix, including its predation risk and resource offering (PREVEDELLO; FORERO-MEDINA; VIEIRA, 2010; PREVEDELLO; VIEIRA, 2010b). The distances to which species can perceive their environment through their senses is defined as the "perceptual range"

(DOHERTY; DRISCOLL, 2018). In general, a heterogeneous matrix will offer more resources to more species, such as food availability, refuge, nesting sites, and protection from predators (PREVEDELLO; VIEIRA, 2010b). Finally, the matrix can hinder animal movement through human disturbances such as domestic animals, farming operations, or roadkill (FORMAN, 1995).

Habitat amount and landscape connectivity are known to be important for species persistence (BRONDIZIO et al., 2019; PREVEDELLO; VIEIRA, 2010b). It is also important to understand the relationship of biodiversity with different types of land use that make up an anthropogenic matrix. It is often assumed that a matrix type having vegetation structure - height and density - that is similar to that of the natural habitat will have a lower impact on biodiversity in the natural habitat than a matrix type with a very different vegetation structure from the natural habitat (ASSIS et al., 2020; BOESING; NICHOLS; METZGER, 2018; PREVEDELLO; VIEIRA, 2010b; RUFFELL; CLOUT; DIDHAM, 2017). A forest environment that a matrix with a similar structure was more favorable to forest species. However, in most studies of this idea, the natural habitat of interest was a forest. It is thus not clear whether the idea applies to other habitat types such as grassland (EYCOTT et al., 2012).

The question of what constitutes a biodiversity-friendly matrix type is highly relevant in the Brazilian Savanna, or Cerrado (EYCOTT et al., 2012). The Cerrado biome is a hotspot for biodiversity loss (MYERS et al., 2000b) due to a very high rate of deforestation of its native vegetation - forests, savannas, and grasslands (SOUZA et al., 2020). This biome has converted almost 50% of its natural area into different land covers, such as pasture, crops, and silviculture (SOUZA et al., 2020). The pastures are usually dominated by introduced grasses, specially Urochloa decumbens and Urochloa humidicola (CAVA et al., 2018). Major crops are soy, corn, and cotton (BOLFE et al., 2016), and the major form of silviculture is Eucalyptus species, with Pinus spp. and Teca (Tectona grandis) also planted in smaller amounts (IBÁ, 2020). How these different matrix cover types affect biodiversity in the three main Cerrado natural habitats is still unclear.

In this paper, we address this question using small mammals - small rodents and marsupials - as our study group. These species perform a variety of ecosystem functions including serving as prey, mesopredators, seed dispersers, seed predators, and vectors of diseases (PREVEDELLO; FORERO-MEDINA; VIEIRA, 2010). In accomplishing these functions, they commonly move through the landscape, making the role of the matrix highly relevant to their success. We ask two questions: (1) Does matrix type affect the richness of small mammals in different Cerrado natural habitats? And (2) Does matrix type change the species composition of small mammals in different Cerrado natural habitats?

For the first question, we have two opposing hypotheses. (1) Additional habitat hypothesis: a matrix type whose vegetation is more similar to the habitat of interest is more likely to provide additional habitat for the species associated with that habitat type, then, the matrix type will house (some of) those species. More of these species will then occur at a habitat site in a landscape containing more of that matrix type because the landscape will effectively contain more habitat, even if the quality is lower than the natural habitat. Therefore, we expect higher species richness at habitat sites in landscapes where the matrix is dominated by cover types most similar in vegetation structure to the habitat type of interest. (2) The spillover hypothesis: a matrix type whose vegetation is more similar to a different habitat type (different from the habitat of interest) will provide habitat for and house species associated with that different habitat type. More of these species will then "spill over" into a habitat site in a landscape containing more of the matrix whose vegetation structure is like that of the different habitat types. For example, in this case, the pasture is more like grassland and will host some grassland species. Then, the grassland species hosted in pasture can spill over into forest. Therefore, we expect higher species richness in habitat sites that are in landscapes containing more matrix of the type that is most different in vegetation structure from the habitat type. If both hypotheses are true or if neither hypothesis is true, then we might expect no effects of matrix type on species richness.

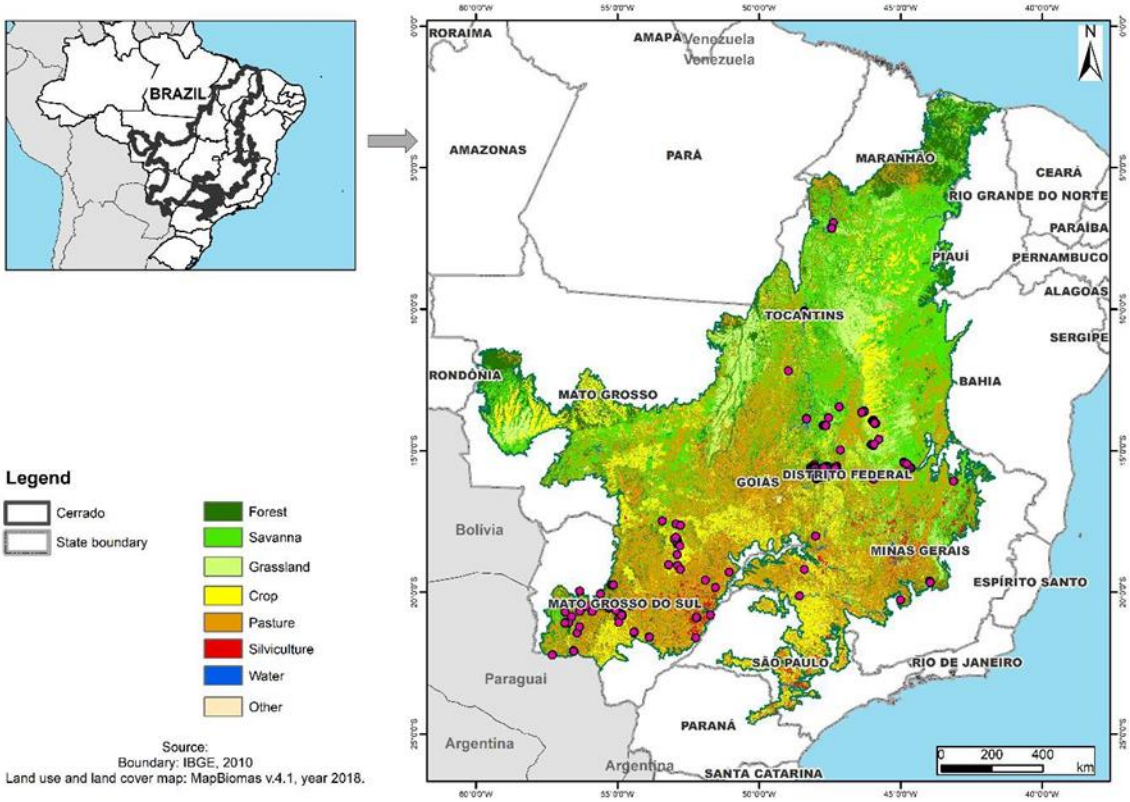
For the second question we predict an effect on species composition of spillover of species from the matrix into natural habitat patches (whether forest, savanna, or grassland patches). This will shift the species composition to reflect the species typically associated with the cover types in the matrix surrounding the habitat patch. Specifically, small mammals in the Cerrado roughly fall into three groups - forest species, savanna and grassland species, and species that use all types of habitats (PAGLIA et al., 2012). Many savanna species also live in native grassland (PAGLIA et al., 2012). Some forest species can use silviculture as habitat and some savanna species can use pasture and some crops as habitat. Therefore, we expect more forest species in the Cerrado natural habitats when the matrix is dominated by silviculture than when it is dominated by crops or pasture, and we expect more savanna species in Cerrado natural habitats when the matrix is dominated by crops and pasture than when it is dominated by silviculture. In contrast, variation in matrix composition should not affect the number of species that use all three types of habitats.

6.2 Material and methods

6.2.1 Study area

The Cerrado biome occupies approximately 2 million km² or a fifth of Brazilian territory, and it is located mostly in the Southeast and Midwest of the country (Figure 6.1). In 2018, the agriculture area in the Cerrado was 250,505 km², the pasture area was 609,761 km², and the native coverage was 1,056,782 km² (SOUZA et al., 2020). The annual temperature averages 22 - 23ºC and the average annual precipitation is 1,200 - 1,800 mm. The Cerrado has a seasonal tropical climate with dry winters. During the dry season, it is common for vegetation to lose its leaves, accumulating dry biomass on the soil. This accumulation of biomass benefits the spread of fire, which is part of the natural dynamics of the Cerrado biome (KLEIN et al., 2002).

Figure 6.1. Distribution of the sampling points for small mammals in the Cerrado biome.



Source: The author.

6.2.2 Data collection

We obtained the small mammal data through from a partnership with researchers from the Universidade Federal de Lavras, the Universidade Federal de Santa Maria, the Universidade de Brasília, the Universidade Federal do Rio de Janeiro, and the Universidade Federal de Uberlândia. This effort resulted in 176 field sampling points distributed across the Cerrado in habitat patches representing the different natural vegetation types, which were situated in different landscape contexts with different types of matrices (Figure 6.1). Initially, we had 235 sampling points: 72 in forest, 139 in savanna, and 26 in grassland. We then excluded some points to eliminate points with less than 3 km in a linear distance from another sampling point. Our final set of points included 62 points in forest, 79 in savanna, and 26 in grassland. We computed richness and species composition for each sampling point. We also calculated the sampling effort for each point, as the number of traps times the number of nights of trapping. We then divided the total richness of the sampling point by the sampling effort. We quantified the landscape context within 2km from each sampling point. This distance was previously determined as the scale at which landscape variables most strongly influence small mammals in the Cerrado (MELO et al., 2017b). Within each landscape, we obtained the percentage of forest, savanna, grassland, silviculture, crops, and pasture using spatial data from the same year as the small mammal sampling for that sampling point.

The land cover data were taken from the Brazilian Annual Land Use and Land Cover Mapping Project (MapBiomas, version 4.1) (SOUZA et al., 2020). MapBiomas is a project that uses a temporal series of Landsat images (spatial resolution of 30 m) to classify land use and land cover of the Brazilian biomes, using machine learn algorithms. The dataset contains 33 classes for land use and land cover, and the temporal resolution is 1 year. MapBiomas data are freely available at the website < https://mapbiomas.org/ >. We used the map for the Cerrado biome. We renamed and reclassified the classes of MapBiomas as follows: Forest Formation as "forest"; Savanna Formation as "savanna"; Grassland Formation as "grassland"; Annual and Perennial Crops and Semi-perennial Crops as "crops"; Forest Plantation as "silviculture"; and Pasture as "pasture".

6.2.3 Does matrix type affect the richness of small mammals in different Cerrado natural habitats?

To test our predictions related to Question (1), we built three General Linear Models (GLMs), one for sampling points in forest, one for points in savanna, and one for points in grassland. The response variable was small mammal richness, and the landscape predictors were the amount of that same natural cover type (the "focal" habitat type) and the amount of each of the three matrix types (pasture, crop, and silviculture) within the 2-km radius landscapes surrounding the sampling points. The amount of the focal habitat type was included to control for the strong expected effect of habitat amount on species richness (FAHRIG, 2013). Thus, the model predicting species richness in forest patches had the predictor variables percentage of the landscape in forest, pasture, crops, and silviculture. The model predicting species richness in savanna patches had the predictor variables percentage of the landscape in savanna, pasture, crops, and silviculture. And the model predicting species richness in grassland patches had the predictor variables percentage of the landscape in grassland, pasture, crops, and silviculture.

6.2.4 Does matrix type change the species composition of small mammals in different Cerrado natural habitats?

To test our Question (2), we did a literature review to classify all mammal species in our database according to the type of Cerrado land cover they use as habitats (Appendix B.1). From this classification, we verified that most species that use grasslands also occur in savannas. Our final classification grouped the small mammals into three categories: forest species, savanna and grassland species, and species that use all three types of Cerrado natural habitat. So, we obtained the three categories of species in a presence/absence matrix per site, hereafter, we are referring to this matrix as species composition.

To assess the relationship between species composition and land use cover we performed the PERMANOVA analysis - Permutational Multivariate Analysis of Variance Using Distance Matrices, using the function Adonis from the vegan package in R. This analysis is useful for our type of data because it allows the comparison of two matrices. It partitions distance matrices among sources of variation and fits linear models to the distance matrices. The Distance-based multivariate linear model analysis (DistLM) evaluated if the response variable (species composition represented by a presence/absence matrix of the three categories of small mammals per site) responds to the explanatory variables (percentage of the natural habitat, crops, pasture, and silviculture). We used two matrices: 1 - a presence/absence matrix of the three categories of small mammals per site; 2 - the predictor variables per site. The formula is similar to a general linear model expression (e.g., species composition ~ %forest +%savanna + %grassland + %pasture + %crops + %silviculture + sampling effort). To predict the species composition in forest patches, our model considered the percentages of forest, pasture, crops, and silviculture in the landscape as predictors. Similarly, to predict composition in savannas, the percentage of savanna, pasture, crops, and silviculture in the landscape were explanatory variables. And finally, to predict composition in grasslands, the percentage of grassland, pasture, crops, and silviculture were explanatory variables.

6.3 Results

The mean species richness considering all the sample points is 2.615 (median 2 and variance 12). The average species richness in the forest is 3.57 (median 3 and variance 10), in the savanna is 4.1 (median 4 and variance 11) and in the grassland is 1.69 (median 1 and variance 7).

The mean percentage of forest cover considering all the sample points is 23.56% (median 14.66% and variance 87.60%), for the savanna, the mean percentage is 20.36% (median 11.66% and variance 87.36%), and for grassland, the mean percentage is 21.71% (median 6.13% and variance 98.30%). Considering all the sampling points, the mean percentage of pasture coverage is 25.67% (median 19.45% and variance 87.58%), for crops 2.36% (median 1% and variance 83.85%) and for silviculture, the mean is 2.15% (median 1% and variance 62.18%). The correlations among the six land cover classes were low, all less than 0.5.

6.3.1 Does matrix type affect the richness of small mammals in different Cerrado natural habitats?

Overall, the effects of surrounding land cover on small mammal species richness at sampling sites were weak and uncertain (generally not statistically significant)

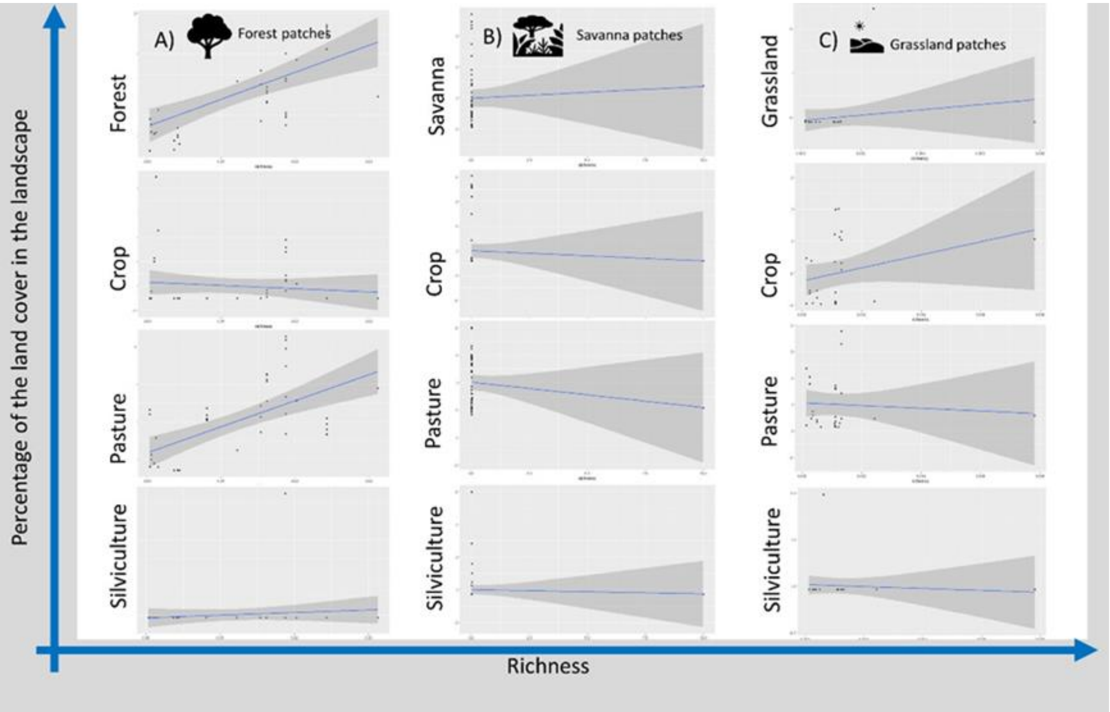
(Table 6.1, Figure 6.2). Based only on the coefficients associated with the matrix types, we found mixed results for the Additional Habitat hypothesis. For forest habitat, although the coefficient for silviculture was positive, the coefficient for pasture was even stronger. For the savanna habitat, the crop had the smallest negative coefficient of the three matrix types as predicted, but the difference among them was not large. Finally, the strongest support for the first hypothesis was for grassland habitat where the coefficient for the crop was positive and the largest of the coefficients for the three matrix types. Consistent with the Spillover hypothesis, we observed a strong positive effect of the percentage of pasture on species richness in forest sites, suggesting spillover of pasture species into forest sites (Table 6.1, Figure 6.2). However, we did not observe any effects of the matrix on species richness in savanna and grassland sites.

Table 6.1. Generalized linear model tests for the effects of the percentage of matrix type on small mammal species richness.

Predictable variables	Estimate	Std. Error	t - value	p - value
		Forest sites		
Intercept	-4.71	0.10	-45.66	< 2e-16 *
Forest	0.44	0.09	4.71	3.12e-05 *
Crop	-0.14	0.14	-1.02	0.31
Pasture	0.55	0.10	5.73	1.23e-06 *
Silviculture	0.11	0.08	1.40	0.17
		Savanna sites		
Intercept	-2.88	2.03	-1.42	0.16
Savanna	-0.10	0.61	-0.16	0.87
Crop	-0.92	3.58	-0.26	0.80
Pasture	-1.47	1.46	-1.01	0.32
Silviculture	-1.47	4.58	-0.32	0.75
		Grassland sites		
Intercept	-6.86	6.31	-1.09	0.28
Grassland	0.43	6.47	0.07	0.95
Crop	0.25	4.65	0.05	0.96
Pasture	0.06	6.38	0.01	0.99
Silviculture	0.00	8.30	0.00	1.00

Standardized slope coefficients (Estimate), standard errors (Std. Error), t-value, and p-value in the generalized linear model tests for the effects of the percentage of matrix type - crop, pasture, and silviculture - within 2 km of small mammal sampling points, on small mammal species richness in sample points in forest (i), savanna (ii), and grassland (iii). In each case, the percentage of the given habitat type in the landscape is also included in the model.

Figure 6.2. The richness of small mammals in (A) forest sites, (B) savanna sites, and (C) grassland sites vs. the percentage of that cover type as well as, crops, pasture, and silviculture in the landscapes surrounding small mammal sample sites.



Source: The author.

6.3.2 Does matrix type influence the species composition of small mammals in different Cerrado natural habitats?

Irrespective of the habitat type where the sample was taken, there are more mammal forest species in sites surrounded by more pasture and there are fewer forest species in sites surrounded by more silviculture. The effect of the crop in the matrix on forest species depends on where the small mammals were sampled.

There are fewer savanna/grassland species in savanna sites surrounded by more savanna, but there are more savanna/grassland species in forest sites surrounded by more forest and in grassland sites surrounded by more grassland. There are more savanna/grassland species in forest sites and savanna sites surrounded by more pasture. There are more savanna/grassland species in savanna sites and grassland sites surrounded by more silviculture.

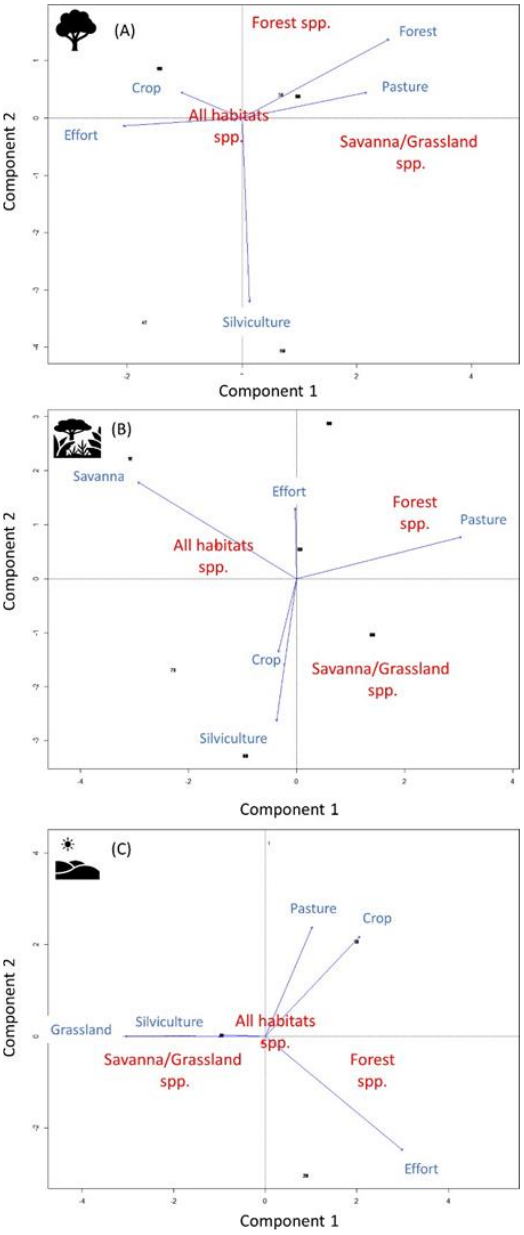
The hypotheses of a spillover of species from the matrix into habitat patches (whether forest, savanna, or grassland patches) shifting the species composition was partially supported by our results (Table 6.2, Figure 6.3). When the matrix was dominated by pasture, we found a shift in species composition in forest patches (Table 6.2, Figure 6.3) with an increase of savanna and grassland species, and more forest species in savanna sites and grassland sites (Table 6.2, Figure 6.3). When the matrix is dominated by crops, we found fewer savanna/grassland species in forest sites; fewer forest species and more savanna/grassland species in savanna sites; and more forest species and fewer savanna/grassland species in grassland sites. In addition, in landscapes dominated by forest, there are more forest species into forest patches (R2 = 0.11; r = 0.001); in landscapes with more savanna, we found more savanna/grassland species into savanna patches (R2 = 0.13; r = 0.001); and in landscapes with more grassland, we found more savanna/grassland species into grassland patches (R2 = 0.21; r = 0.010).

Table 6.2. Results from the distance-based linear modeling (DistLM) tests for the independent effects of matrix type on small mammal species composition in forest, savanna, and grassland.

Predictor variables	Df	MeanSqs	F.Model	R2	r-value (>F)
Forest sites					
Forest	1	1.51	8.01	0.11	0.001*
Crop	1	0.20	1.06	0.01	0.353
Pasture	1	0.75	3.99	0.05	0.003*
Silviculture	1	0.44	2.34	0.03	0.039
Effort	1	0.42	2.22	0.03	0.044
Residual	54	0.19		0.75	
Total	59			1.00	
Savanna sites					
Savanna	1	1.84	13.32	0.13	0.001*
Crop	1	0.16	1.15	0.01	0.324
Pasture	1	0.67	4.86	0.05	0.002*
Silviculture	1	0.38	2.72	0.03	0.105
Effort	1	0.77	5.61	0.06	0.014*
Residual	73	0.14		0.72	
Total	78			1.00	
Grassland sites					
Grassland	1	0.91	6.66	0.21	0.010*
Crop	1	0.31	2.26	0.08	0.193
Pasture	1	-0.03	-0.25	-0.01	0.974
Silviculture	1	0.14	1.01	0.03	0.353
Effort	1	0.20	1.45	0.05	0.257
Residual	20	0.14		0.64	
Total	25			1.00	

The response variable was a matrix of presence-absence of species per site. Predictor variables were the percentage of the forest, savanna, grassland, pasture, crop, silviculture within the landscapes, and the sampling effort for each area. We used the standardized coefficients to test the predictions.

Figure 6.3. The results from Distlm for the composition of small mammals. The small mammals were classified into Forest species, Savanna/Grassland species, and All habitat species. Species composition was evaluated within (A) forest, (B) savanna, and (C) grassland patches. The black dots represent the sample points. For example, in the plot (A) we observe that savanna/grassland species (in red) are related to an increase in percent pasture (blue arrow), forest species are related to the increase in percent forest, and the species that use all types of habitats are not related to any land cover.



Source: The author.

6.4 Discussion

Matrix quality is an important factor to implement a more friendly human-dominated landscape for conservation purposes (ARROYO-RODRÍGUEZ et al., 2020), but the importance of the matrix structure in determining matrix quality was not so relevant to mammals species richness in the Cerrado. In opposition to the current association of the matrix structure as a good indicator to increase richness in human-dominated landscapes (EYCOTT et al., 2012), we rejected our first hypothesis (Additional Habitat hypothesis) but accepted the second one (Spillover hypothesis). So, in accordance with our prediction of the second hypothesis, we found more species in habitat sites containing more of the matrix type with different vegetation structures in the surrounding landscape. This result was particularly strong in forest patches.

The response of the matrix structure to species richness inside patches was not uniform in different habitat types: forest, savanna, and grasslands. We only observed an increase of richness in forest patches associated with more pasture in the matrix. The matrix type did not show effects on the richness of small mammals within savanna or grasslands. Again, this has an important implication when determining optimal landscapes for conservation using the matrix structure or matrix biomass as an indicator of matrix quality, as seen in previous studies' recommendations (REIDER; DONNELLY; WATLING, 2018; RUFFELL; CLOUT; DIDHAM, 2017). To small mammals in other biomes forest habitats, the structure of a matrix showed to be an important factor to improve matrix quality (ASSIS et al., 2020; UMETSU; PAUL METZGER; PARDINI, 2008), but this pattern did not show relevance in this study case. At least, our results show that when habitat structure is not homogeneous in the natural landscape, the matrix structure or biomass is not an indicator of the matrix quality for small mammal species.

The effect of the matrix on species composition is dependent on the matrix type and species habits. We observed that, regardless of the habitat type where the sample was taken, there are more forest species in sites surrounded by more pasture and fewer forest species in sites surrounded by more silviculture. The impact of the amount of crop in the matrix on forest species depends on where the small mammals were sampled. This suggests either that forest species can move safely through the pasture or that they find additional resources in the pasture or both. In turn, crops or silviculture do not provide resources or a safe movement route for forest species. We observed a similar pattern to savanna/grassland species: more savanna/grassland species in forest sites and savanna sites surrounded by more pasture. But in opposite to forest species, we also observed more savanna/grassland species in savanna sites and grassland sites surrounded by more silviculture. From this, we suppose that pasture provides resources for savanna/grassland species. Also, savanna/grassland species may be able to move through silviculture and/or may find resources there. These results are not in agreement with the literature review (PREVEDELLO; VIEIRA, 2010b; UMETSU; PAUL METZGER; PARDINI, 2008) that usually considers that a matrix with different strata has more resources to species than open fields matrices. But that it is important to highlight that the strata also can act as an obstacle to the species crossing the matrix. It was observed for example that the strata can modify the perception of a species from a patch from distance (FORERO-MEDINA; VIEIRA, 2009). There is a trade-off between the risks and benefits offered by the matrix during the movement (ZOLLNER; LIMA, 2005), and our results suggest that for the Cerrado species, an open matrix offers a better route for forest species movement.

Another perspective about our results is concerning how species composition changed accordingly to the matrix type. The increase of pasture in the matrix resulted in an increase of savanna/grassland species in the forest. This means that the increase of forests resulted in a spillover from different species into the forest. This effect of introducing species that are not natural from one habitat type with the presence of a different matrix type is one predictable impact of the matrix (DRISCOLL et al., 2013). The effect that we found on the small mammals' community can also be seen in the increase of alien species and fire (DA ROSA et al., 2017; NOGUEIRA et al., 2017). Also, when pastures were the main matrix type, there was an increase in forest species inside the savanna. We did not observe any changes according to the matrix in the species composition inside grasslands.

Considering the amount of native Cerrado in the landscape, forest and savanna/grassland species answered differently. Forest species answered positively to the increase of forest in the landscape. We found fewer savanna/grassland species in savanna sites surrounded by more savanna, but there are more savanna/grassland species in forest sites surrounded by more forest and in grassland sites surrounded by more grassland. This result suggests that there are no small mammal species associated only with savanna. From our results, the "savanna/grassland" category of species may be truly a set of species that are found in both forest and grassland but not in the savanna. We observed that species composition within savannas is also dependent on the mosaic of different types of Cerrado on the landscape and not just on the amount of savanna around it. Indeed, the species composition inside the savanna was considered with fewer species whose occurrence is restricted to it (CÁCERES et al., 2010a; PAGLIA et al., 2012). This result shows that, in this study considering different types of savanna, the matrix structure is not a good indicator of the matrix quality. Also, the matrix type does not show the effect on the richness of small mammals within grasslands. Another possible explanation for our richness results is that Cerrado natural formation has structure variations, and it is a mosaic of forest, savanna, and grasslands (RATTER; RIBEIRO; BRIDGEWATER, 1997b). This fact justifies that structure itself would have a small influence on richness inside Cerrado patches.

For all groups of species considered - forest species, savanna/grassland species, and species that use all types of habitats - the increase in habitat was correlated with the increases in its richness. An increase of forest species was observed in forest patches with more forest in the landscape; species that use all types of habitats within savanna increased with more savanna in the landscape; savanna/grasslands species increased with more grasslands in the landscape. Our results highlight what already is a consensus on the importance of habitat amount to conservation (FAHRIG, 2003). A design proposal for a more friendly landscape includes (i) determining a threshold of natural habitat to be kept, which depends on the matrix quality, and (ii) keeping small patches to improve connectivity (ARROYO-RODRÍGUEZ et al., 2020). We observed the importance of habitat amount for all types of Cerrado natural habitats, but we showed the impact of matrix on increasing the introduction of species into natural habitats, not on minimizing the effect of habitat loss.

Overall, the composition of the matrix is homogeneous, and because it does not have the same amount of resources as native areas have, this can explain why matrix composition is not a good predictor of quality (FORMAN, 1995). Even though those environments have a structure similar to the native areas, they do not have enough resources for most native species. Also, the Cerrado's natural formation has structure variations and is a mosaic of forest, savanna, and grasslands. This fact justifies that structure itself would not influence richness inside the Cerrado patches.

6.5 Conclusion

We verified the interference of the matrix type to the small mammal's community inside natural patches. The matrix did not reduce the impacts of habitat loss, instead, we observed the negative effects of the matrix introducing species from different environments into the habitat. This highlights the importance of considering the matrix type to design a more conservation-friendly landscape, not only to increase permeability but to consider the impacts of the matrix type on natural communities' composition. In our results, the structure of the matrix was not a good indicator of resources. Overall, we did not support the idea that a matrix with a structure similar to habitat has the lowest impact on species richness in the habitat. We suggest to future studies investigate more deeply the relationship between matrix structure and matrix resources. We also suggest further detailed studies about the impacts of different types of matrices on species or communities within non-forest environments.

7 MODELING THE RESPONSES OF SMALL MAMMALS TO LAND USE AND COVER CHANGES IN CERRADO PHYTOPHYSIOGNOMIES

7.1 Introduction

The Millennium Ecosystem Assessment (MEA) defined the five major drivers of biodiversity loss as habitat change, climate change, invasive species, overexploitation, and pollution (MILLENNIUM ECOSYSTEM ASSESSMENT PROGRAM, 2005). For terrestrial species, habitat loss is one of the three main drivers of biodiversity loss (MYERS et al., 2000b), and the majority of publications studying the drivers of habitat loss is dedicated to understanding its impact (MAZOR et al., 2018). Despite this, the interactions of the land cover changes and the losses of biodiversity during the time are still of poor understanding (KUUSSAARI et al., 2009). Part of the reason for this is because the time lag between changes in the landscape and the response of biodiversity causes failures to observe extinctions following habitat loss (HALLEY; SGARDELI; TRIANTIS, 2014).

Between losses of habitat and the response of biodiversity, there is a time lag called relaxation time (KUUSSAARI et al., 2009). The relaxation time may influence the observation of the number or proportion of populations expected to eventually become extinct, or decline, after habitat change. This proportion of the population expected to decline or become extinct in a metapopulation is the definition of extinction debt (KUUSSAARI et al., 2009).

Testing extinction debt is especially challenging because of difficulties in the long-term monitoring of biodiversity in dynamic landscapes, determining the spatial and time resolution to sample, and obtaining maps in appropriate time resolution (HALLEY; SGARDELI; TRIANTIS, 2014). Alternatively, the methods to estimate extinction debt include sampling in one-time and multiple-time maps (LIRA et al., 2012) or using conceptual models to simulate scenarios of interactions and land cover changes and species (KUUSSAARI et al., 2009).

The problems in monitoring biodiversity make the majority of studies on the extinction debt be concentrated on plants, despite animals show more vulnerable to the effects of relaxation time (KUUSSAARI et al., 2009). When we consider mammals, the interaction between species and landscape needs to consider that they can recognize the environment differently and this perception affects their ability to move across the landscape and to persist in human-modified areas (PREVEDELLO; VIEIRA, 2010b).

Considering the difficulties in sampling small mammals in long-term monitoring, models present a good solution to understand this interaction and study the impact of relaxation time in small mammal populations. Among the techniques of modeling useful to this type of study (MARTIN; FAHRIG, 2016; ROCHA et al., 2021), the Agent-based Model (ABM) is interesting because it can simulate interactions among species decisions and space. In the ABM the phenomenon is understood from the agents and the interaction between them (WILENSKY; RAND, 2015). The search for patterns that reflect behavior is a way of defining the rules of agents and their interactions (GRIMM et al., 2005a). Agents are autonomous elements that possess common property, state, and behavior that can be simulated computationally (WILENSKY; RAND, 2015).

In this study, we propose an ABM to simulate the interactions between small mammal populations and a human-modified landscape through time. We used small mammals as agents to incorporate the behavior and the ability to make decisions to understand how landscape change affects small mammals' perception of an environment. We used different types of Cerrado phytophysiognomies because this biome is a complex mosaic of natural habitats and different human matrices (RATTER; RIBEIRO; BRIDGEWATER, 1997b). We aim to answer how the relaxation time and the extinction debt are observed in the small mammals' community.

7.2 Material and methods

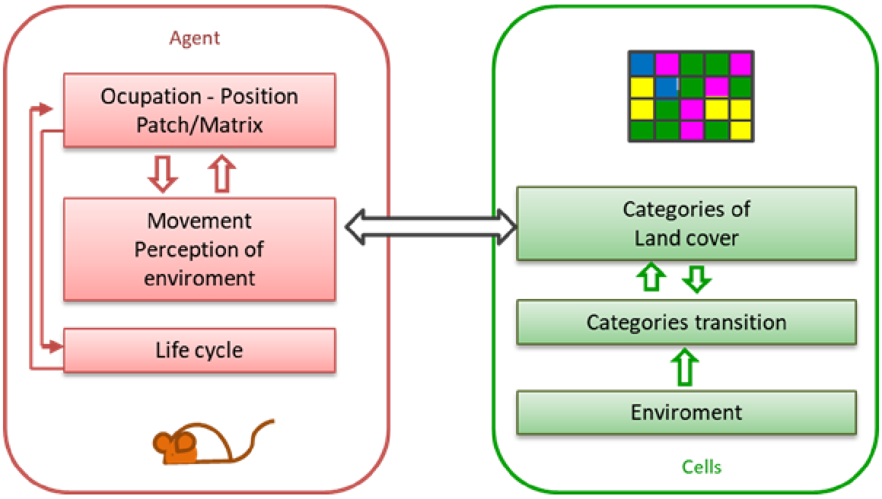
7.2.1 The model

We created an agent-based spatially explicit simulation model – the Small mammals at the Cerrado Changes (SMAC), in the TerraME modeling environment (CARNEIRO et al., 2013) intending to observe the relaxation time and the extinction debt in different types of landscapes. After being published, the SMAC model code will be available on the TerraME platform on Github. We simulated population dynamics and dispersal characteristics in different historic landscape types, varying in habitat amount and types of the Cerrado natural habitats. Then, we submitted each landscape and its population with optimal evolved dispersal characteristics to habitat loss. The code is available in the Appendix C.1.

We used the Cerrado biome as the model overall environment, or forces that drive the behavior and dynamics of all agents or grid cells (GRIMM et al., 2010). The Cerrado biome is one of the Tropical Grassy Biomes (TGB) that includes savannas and grasslands (LEHMMAN; PAR, 2016). Those biomes have some dry periods throughout the year and fire is part of the Cerrado natural cycle (KLEIN et al., 2002). We considered the spatial scale of the extension – 10km x 10 km, and the resolution of 30m. We considered to time scale the extension of 17 years (2000 to 2018) with a daily resolution.

Our model simulates the movement of individuals deciding to cross the anthropogenic matrix or patches of natural habitats. Also, the models include the species' life cycle and decisions in the movement (Figure 7.1). The landscape includes habitat patches and different types of anthropogenic matrices.

Figure 7.1.The ABM conceptual model for the Small Mammals And Cerrado Changes (SMAC).



The model is composed of two major components: the agent and the space (or cells). The agent component reproduces the life cycle of small mammals, and it is placed in a spatial area. The spatial component reproduces the geographical space, where the agent lives, and it is dynamic and changes throughout time. The agent can perceive the environment and decide how to move in the space.

Source: The author.

The model is composed of two major components: the agent and the space (or cells). The agent component reproduces the life cycle of small mammals, and it is placed in a spatial area. The spatial component reproduces the geographical space, where the agent lives, and it is dynamic and changes throughout time. The agent can perceive the environment and decide how to move in the space.

An agent is defined as an autonomous computational individual whose properties and actions are inherent to itself (WILENSKY; RAND, 2015). In this model, we consider mobile agents the individuals of small mammals. This means that the agent will have the behavior pattern defined by the species that which it belongs.

The space component comprises the spatial units, or cells containing information on land use and land cover map, hydrography, and fire. We considered a cellular space with 10km x 10km and 30m resolution. This extension was taken to obtain a representative landscape in Cerrado in which interactions with small mammals can occur. It is important to notice that this landscape is not taken only in a focal point where the small mammal population was sampled, and this is why we did not use the scale of effect. We used the resolution of 30m because it was the finest resolution data of land use classes for Cerrado available, in this case, the Mapbiomas mapping. The ideal would be to study small mammals using even smaller resolutions, however, at this time, MapBiomas provided a suitable land cover mapping to represent the heterogeneity in the landscape with the time resolution needed for the model.

For each cell, it was assigned a class of land use and land cover, information on fire frequency, and the distance of the hydrography as environmental conditions that interfere with the mammals' perception. The choice of the spatial variables was based on the aspects relevant to the small mammals. The land use and land cover maps were obtained to have the heterogeneity necessary to represent the differences interpreted by small mammals during movement or use of the habitat (ASSIS et al., 2022). The fire frequency was obtained because it is a common dynamic in the Cerrado biome and can have an impact on the mortality of small mammals (CAMARGO et al., 2018; MENDONÇA et al., 2015). Finally, we used the hydrography data because it represents a barrier to most small mammal species and can act as a path to species of semi-aquatic habitat (PATTON et al., 2015).

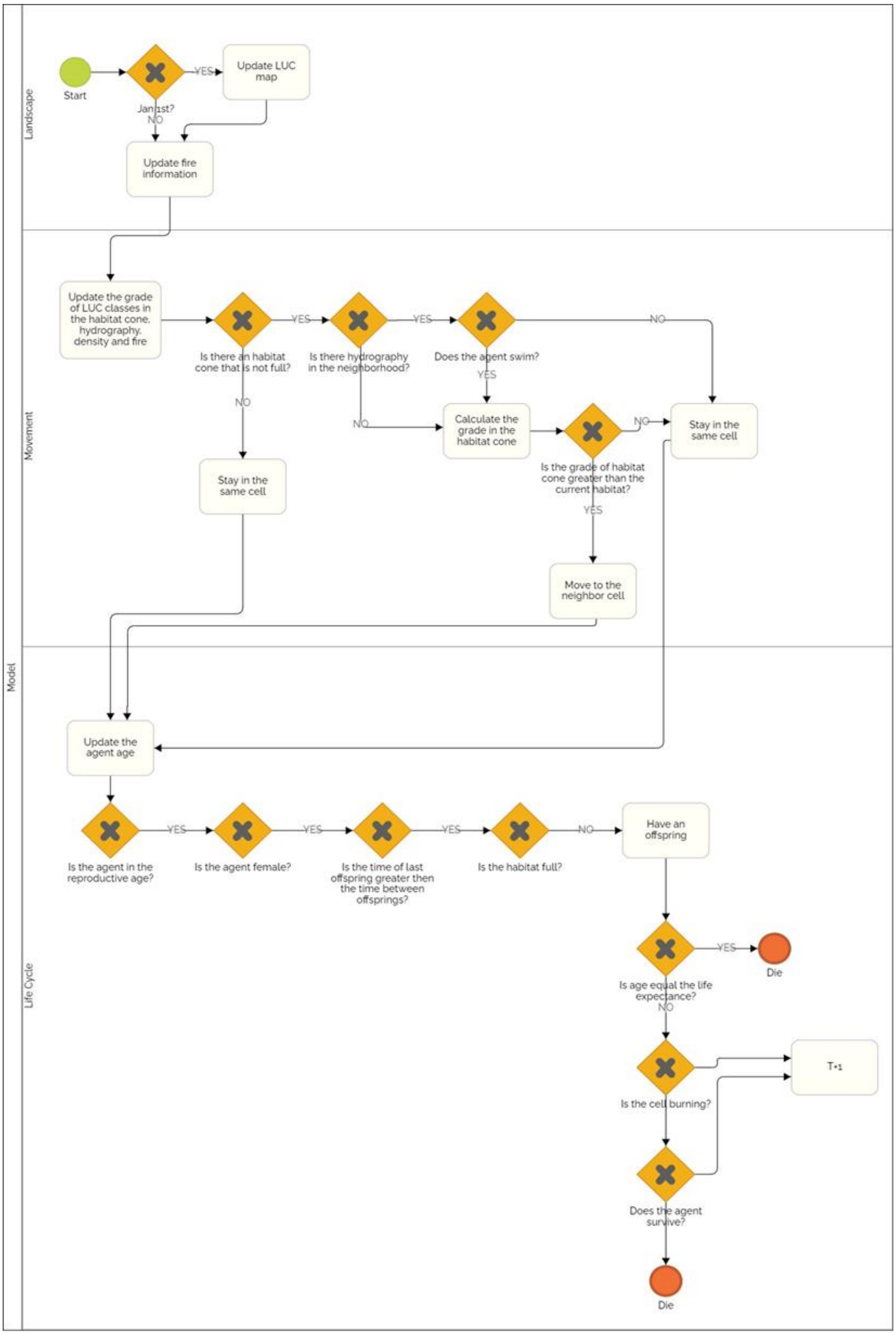
We filled this cellular space with the majority class of land use and land cover from 2000 to 2017, from MapBiomas map v.4.0 (SOUZA et al., 2020, p. 20); with the estimate of minimum distance from the hydrography data (ANA, 2019); and with information about dairy fire occurrence from satellites Aqua and Terra (INPE, 2019). The data from the fire monitoring system are points obtained based on images with 250m of resolution. Because of this, to fill the cellular space, we used a buffer of 250m from the point of the fire data. We filled the cells with fire data using the fire presence as an attribute to each cell that overlaps the buffer of the data source. The time resolution of the fire data is daily, and we consider the period from 2000 to 2017.

In the model, the land use and cover maps are updated annually, and fire data is updated daily. It means that a cell can assume a new class once a year and the fire data can be modified every day of the simulation.

7.2.1.1 Design concepts

The interactions will occur between small mammals and landscape and, among individuals of small mammals. The SMAC model comprises three sub-models: Landscape, Movement, and Life Cycle (Figure 7.2).

Figure 7.2. SMAC Sub-Models and the sequence of events for the simulation model.



Source: The author.

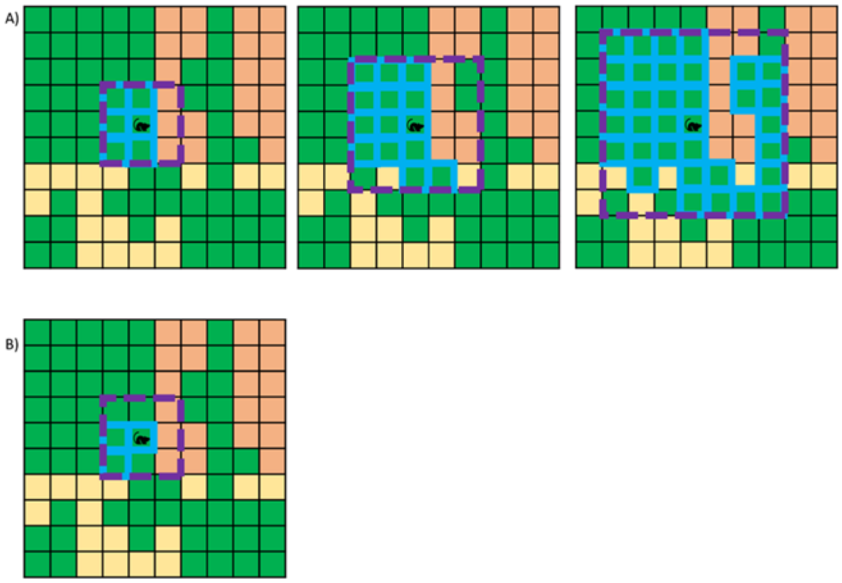
The first sub-model, Landscape, refers to the spatial units. The spatial units have information about land use and land cover, hydrography, and fire data. As the first year of simulation is 2000, all data is obtained initially for this year, and they are updated annually for land use and land cover changes, and daily for fire data.

The second sub-model determines the individuals' Movement. The agent's decision of moving or not is based on habitat preference, disturbs (fire), density, matrix permeability, and barrier (hydrography). The parameters of species preferences, barrier, permeability, and density are described further in Table 7.1. Initially, individuals are in a cell of their habitat preference. Individuals' locations and their habitat are daily updated, and the agent updates its habitat by choosing the number of cells defined by the size of its living area and its area preferences (Figure 7.3).

Table 7.1. Spatial parameters and life cycle parameters for the agents.

Parameter	***Akodon montensis***	***Didelphis albiventris***	***Monodelphis domestica***	***Nectomys squamipes***
Offspring	4	6	8.4	4.5
ReproductiveAge	90	213	180	90
BurningProbability	0.6	0.8	0.5	0.8
BetweenOffspring	120	180	40	105
LifeExpectance	660	300	1170	14
Forest	4	4	4	4
Savanna	3	4	4	3
Grassland	2	4	1	1
Crop	2	1	1	1
Pasture	3	2	1	1
OtherNonVegetatedArea	0	0	0	0
Silviculture	1	2	1	2
Water	0	0	0	4
MosaicAgriculturePasture	2	2	1	1
Wetland	1	1	1	1
Rockyoutcrop	3	2	1	1
Others	0	0	0	0
Density (ind/cell)	0.75	0.27	0.36	0.31
Life area (cells)	7	3	2	3
Perceptual Range (cells)	1	30	1	2
Valid Habitats (to reproduce)	Forest/ Savanna	Forest/Savanna/ Grassland	Savanna/ Grassland	Forest

Figure 7.3. Choice of the cells to integrate into the habitat.

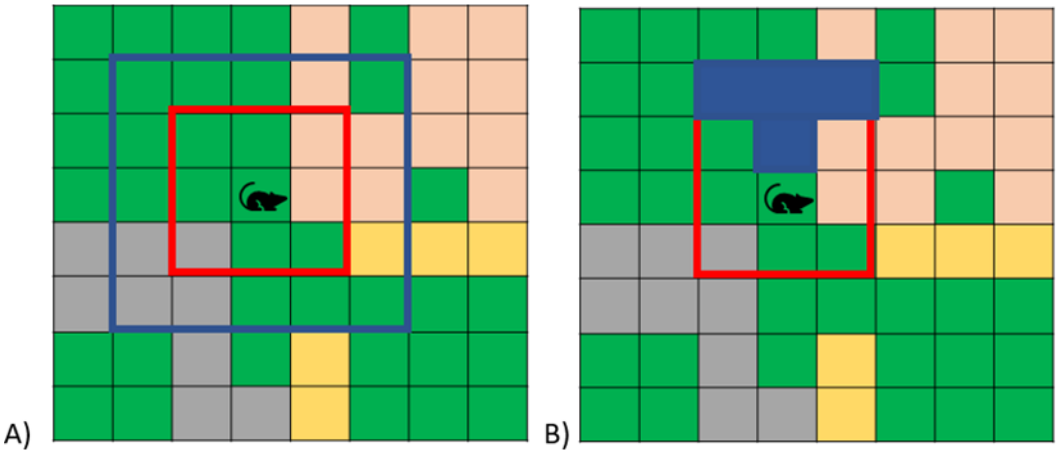


Choice of cells to incorporate in the home range. The agent search in the neighborhood for habitat cells. When there is a habitat cell in the neighborhood, it is incorporated into the home range. Each square is a cell. Green cells are habitat cells. Yellow and rose cells are different matrices cells. The ones with blue contours are cells incorporated into the home range. The purple contour contains all potential cells to be incorporated into the home range in the neighborhood. A) The agent's home range is 33 cells. B) The agent home range is 3 cells.

Source: The author.

In each time step, the agent verifies its neighborhood cells inside its perceptual range determined by the number of cells to obtain information about habitat, matrix, density, fire, and hydrography (Figure 7.4). We determined habitat cones to quantify the cells in the perceptual range in each direction that the agent can move. The decision about moving or not is taken based on the best environmental option. For this, the agents choose the direction to obtain the best habitat quality, low densities of agents, and low densities of burned cells. Also, small mammals cannot cross water bodies (hydrography), with exception of species that are adapted to the aquatic environment and naturally occur associated with water.

Figure 7.4. The framework of small mammals' decision for movement.



The colors green, yellow, rose and gray represent different classes of land use and land cover. The mouse represents an agent. A) In each time step the agent can move for one of the eight neighborhoods (red line), but they can perceive all cells inside the perceptual range in each direction of the habitat cone (blue line). B) The decision of moving for each cell is based on the attributes present in cells inside the blue pyramid. The individual chooses the cell which neighborhood result represents the best choice for itself.

Source: The author.

The parameters (Table 7.1) were obtained for each agent based on the literature review. For each Cerrado species in our database, we searched their parameters in the literature. Then, the parameter value for each specie was estimated from the average of values obtained for the specie.

In each time step, the agent (the individual of small mammal) first checks the density of other agents inside each habitat cone inside their perceptual range. If the density is above the threshold of the species, this habitat cone is discarded as an option to move. Second, the agent checks if there is the presence of fire inside each habitat cone in its perceptual range. If there is fire, the habitat cone is discarded as an option to move. After, the agent checks the presence of hydrography in the neighborhood. If the agent is capable to swim this cell can still be an option for movement, but if the species does not use hydrography, the cell is discarded as an option to move. Then, the agent counts the number of cells of each class of land cover inside each habitat cone in their perceptual range, considering only the remained ones. Each class is ranked based on the preference for each species according to the literature. The agent will decide to move or to stay inside its current habitat according to the sum of the cells inside its habitat cone, choosing the habitat cone with the highest grade.

The third submodel is the Life Cycle model. It begins with natality. There is a birth rate for each agent. We consider a general sexual rate of 50%. We reviewed the literature for each specie to find the number of offspring, the time between two offspring, and the reproductive age for each specie. Then, we calculated the mean for each agent group. Just the agents who are in their natural habitat can reproduce. The reproduction can occur once or more, accordingly to the literature review.

There are two mortality causes in this model: fire occurrence and individual age. All individuals in the model will die when achieving their average life expectance considering the standard deviation for each species' mortality. The life expectance for each agent group was determined after a literature review for each specie. To determine mortality rates caused by fires, we review the literature searching this rate for each specie. Then, for each agent group, we take the mean mortality rate caused by fire. Different from life expectance (days), mortality by fire is a probability value for the individual to die after a fire event inside its cell.

7.2.1.2 Simulation

We started the simulation in 2000 with the land use and land cover map from this year. We distributed 100 agents randomly in the cells according to their habitat preferences. Then, the model ran for 3,650 days before starting to change land cover maps. This time before the land use changes was necessary for the agents to reproduce, occupy the space, and reach stability in the landscape without any changes.

We analyzed 235 sampling points in Cerrado where we had small mammals data collected in a grid of 10 km x 10 km. Then, we selected areas where the small mammals were collected in forests, savanna, and grassland to find landscapes where the losses of habitat were similar throughout time. We selected one landscape with the dominance of forest, one with the dominance of savanna, and one with the dominance of grassland, and found in the worst scenario a loss of around 12% of habitat.

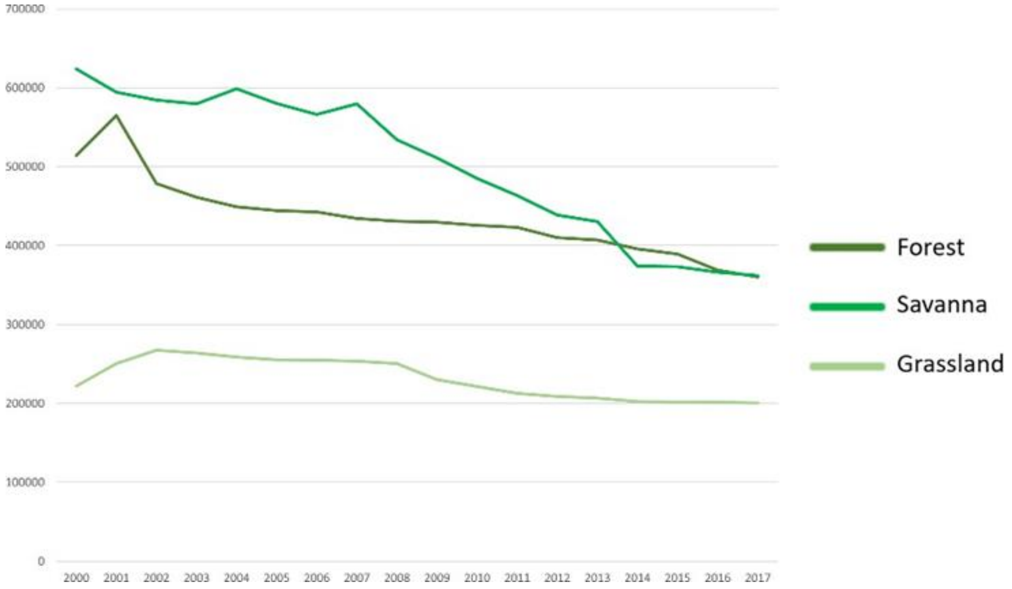
We obtained mammal information collected in 235 sampling points in the Cerrado biome (Chapter 6) and after analyzing it we excluded the points which had a single capture or had only one species in the area. Distributed across the Cerrado in habitat patches, these points represent the different natural vegetation types, which were situated in different landscape contexts with different types of matrices. This effort resulted in an inventory of 53 small mammal species in the Cerrado. We did a literature review on these 53 species to obtain data for the model parameterization. We seek information about how they use the space (density, habitat preferences, type of the Cerrado preferred, home range, and perceptual range, available in Appendix C.2); their life cycle (number of offspring, reproductive age, the time between consecutive offspring, and life expectance, available in Appendix C.2); and additional information (geographic distribution, habit, diet, and size, available in Appendix C.2).

After the literature review, we selected four species with different habitat preferences to test our model: *Akodon montensis* (Rodentia), *Didelphis albiventris* (Marsupialia), *Monodelphis domestica* (Marsupialia), and *Nectomys squamipes* (Rodentia). *A. montensis* is a small sized (30 g – 56 g), widespread, and with a preference for forest understory (PATTON et al., 2015, PAGLIA et al., 2012). D. albiventris is a medium-sized (500 g - 2,700 g) widespread specie that inhabits open and deciduous forest types and is described as an opportunistic species and found in altered habitats (PAGLIA et al., 2012; ALFRED and GARDNER, 2007). M. domestica is a small-sized (67g) specie with occurrence in Atlantic Rainforest, Cerrado, Caatinga, and Pantanal, with the greatest densities in areas of granitic outcrops (PAGLIA et al., 2012; ALFRED and GARDNER, 2007). N. squamipes is a medium-sized rodent (100 g – 400 g), found in Cerrado gallery forests bordering the Atlantic Forest in the Brazilian states of Minas Gerais, São Paulo, and Mato Grosso do Sul, and in Argentina. This specie can use the water streams and is known as “rato d’água” (PAGLIA et al., 2012, PATTON et al., 2015).

7.2.1.3 Simulation experiments

We performed a total of three scenarios, one into a landscape with the dominance of forest, one into a landscape with the dominance of savanna, and one into a landscape with the dominance of grassland. In the landscape dominated by forests, the forest dropped from 42.91% to 31.18% (delta -11.74%) from 2000 to 2018. In the landscape dominated by savanna, the savanna dropped from 35.09% to 22.29% (delta - 12.80%) from 2000 to 2018. And in the landscape dominated by grassland, the grassland dropped from 46.76% to 34.78% (delta -11.97%) from 2000 to 2018 (Figure 7.5). For each scenario we run the model for the four species, *A. montensis*, *D. albiventris*, *M. domestica*, and *N. squamipes*, totalizing 12 simulations.

Figure 7.5. Amount of forest, savanna, and grassland in the three scenarios simulated.



The graphs show the number of cells (y-axis) with each type of land use in the three scenarios simulated throughout time (x-axis).

Source: The author.

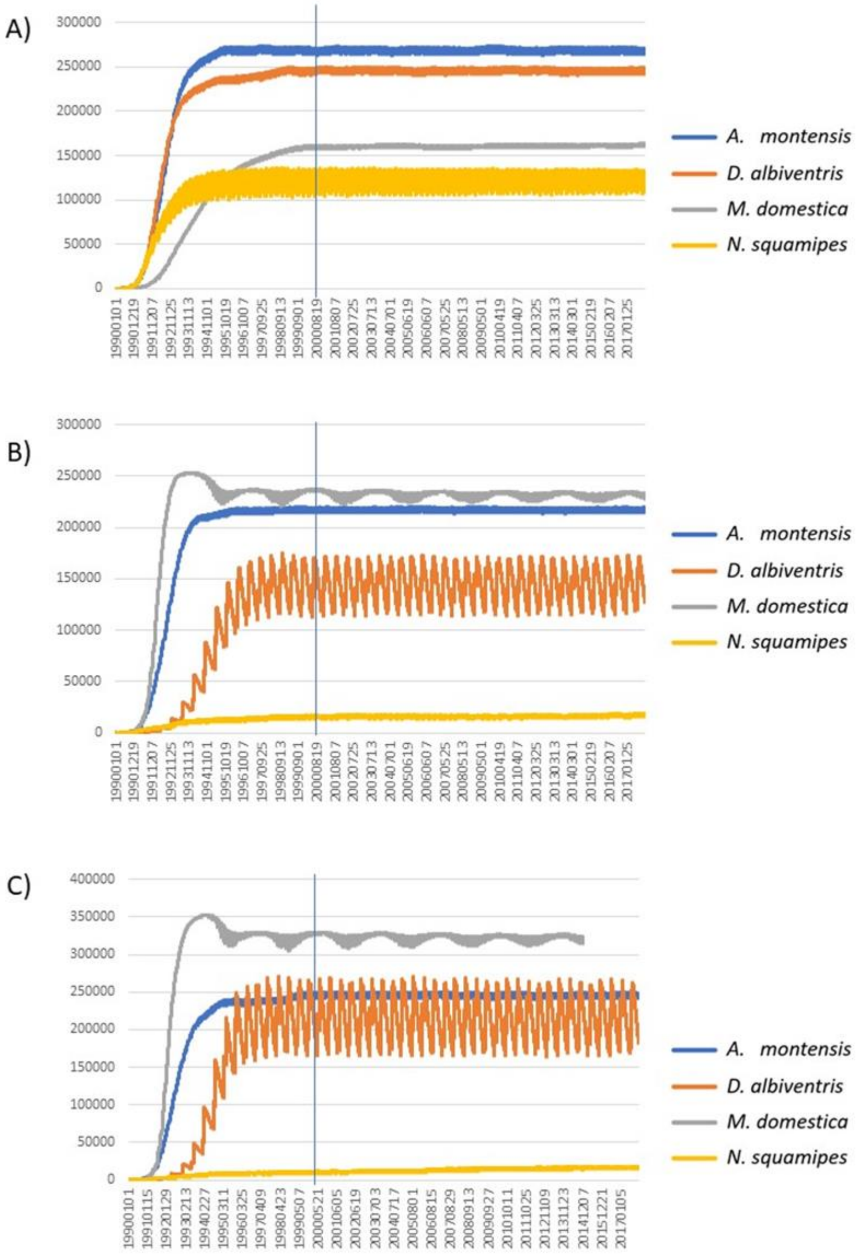
7.2.1.4 Model outputs

For each simulation, we took as results the number of agents in each time step and the number of agents in each land cover in each time step.

7.3 Results

Our results showed that the populations of *A. montensis, D. albiventris, M. domestica*, and *N. squamipes* reached stability to the landscape conditions after 3,650 days, as expected to initiate land cover changes (Figure 7.6). However, we did not find any changes in the population of *A. montensis, D. albiventris, M. domestica,* and *N. squamipes* during or after the habitat loss of forest, savanna, or grassland. We did not observe any changes after habitat loss inside the patches of forest, savanna, or grassland, or inside the landscape (Figure 7.6 and Figure 7.7).

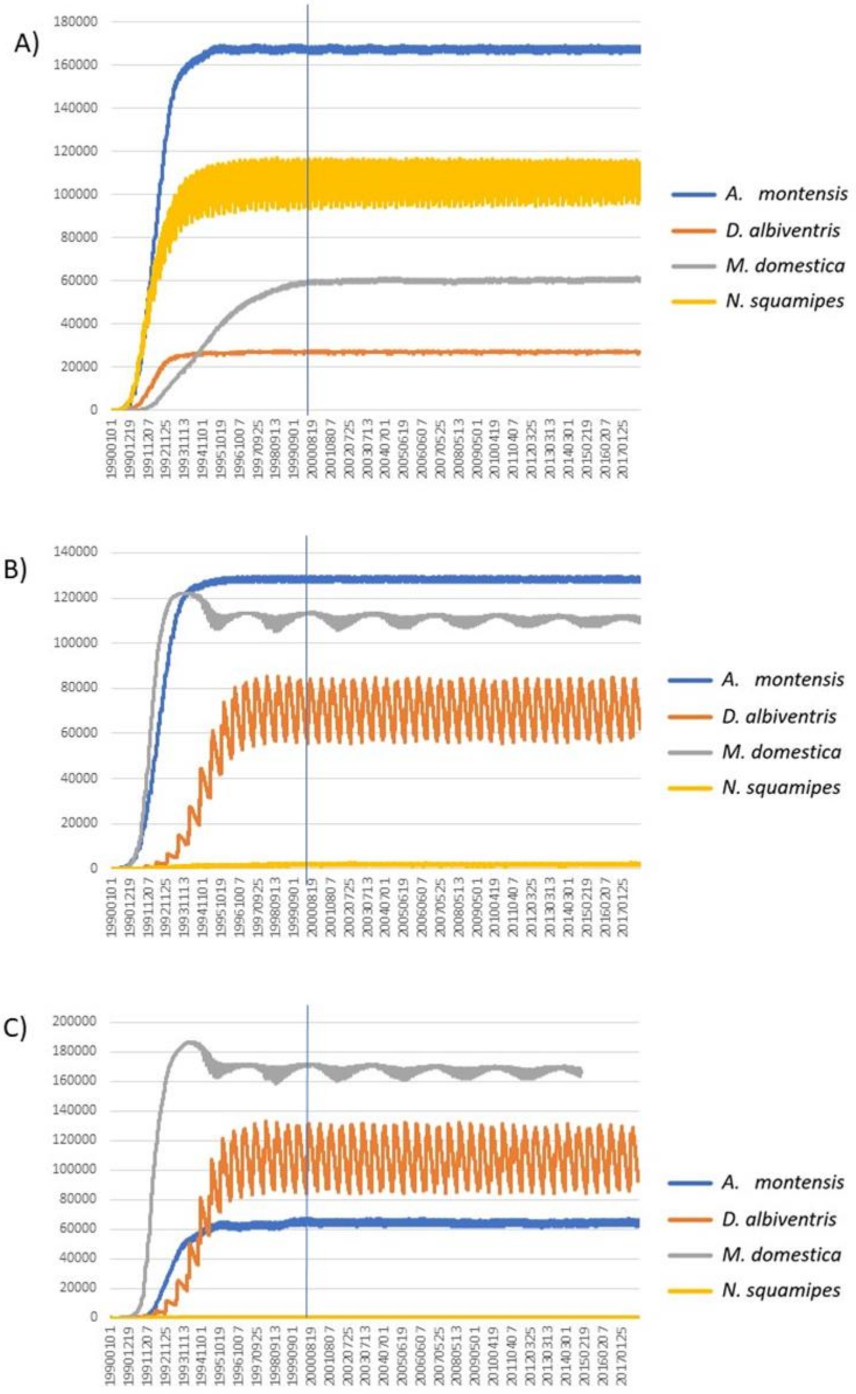
Figure 7.6. Number of agents throughout time in the landscape.



The graphs show each time step in the simulation (X axis) and the number of agents of each species (Y axis) in different colors. A) Landscape with losses of forest; B) Landscape with losses of savanna; C) Landscape with losses of grassland. In letter C), the model to M. domestica ran until 2008.

Source: The author.

Figure 7.7. Number of agents throughout time into the patches.

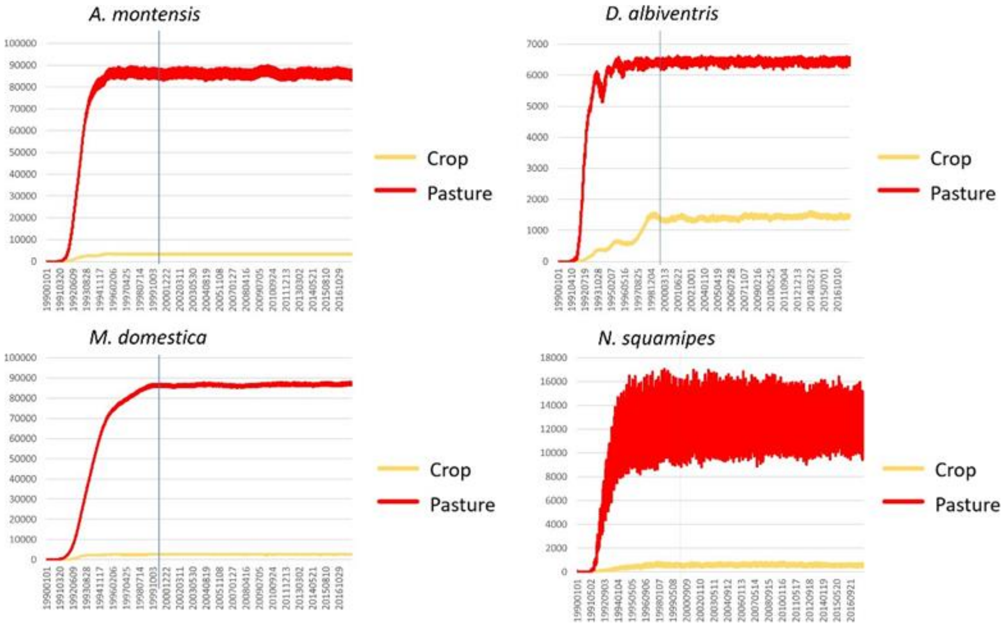


The graphs show each time step (X axis) in the simulation and the number of agents of each species (Y axis) in different colors. A) Patches of forest; B) Patches of savanna; C) Patches of grassland. In letter C), the model to M. domestica ran until 2008.

Source: The author.

We also did not find any changes in the fluctuations of the population *of A. montensis, D. aurita, M. domestica, or N. squamipes* inside the matrix of crops or pasture in the landscape with losses of forest (Figure 7.8), savanna (Figure 7.9), or grassland (Figure 7.10).

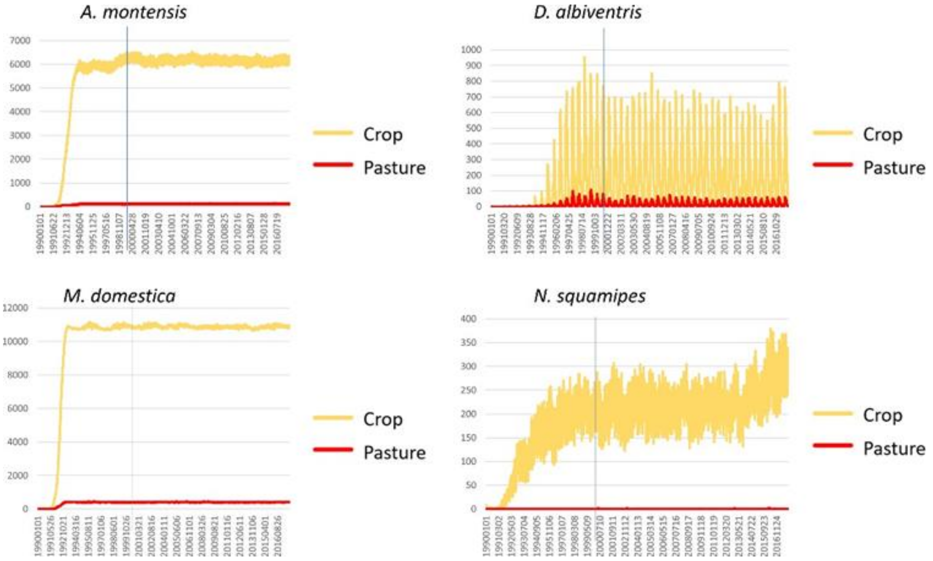
Figure 7.8. Number of agents throughout time into the matrix in the landscape with losses of forests.



The graphs show in the axis each time step in the simulation and the axis y the number of agents of each species in the matrices.

Source: The author.

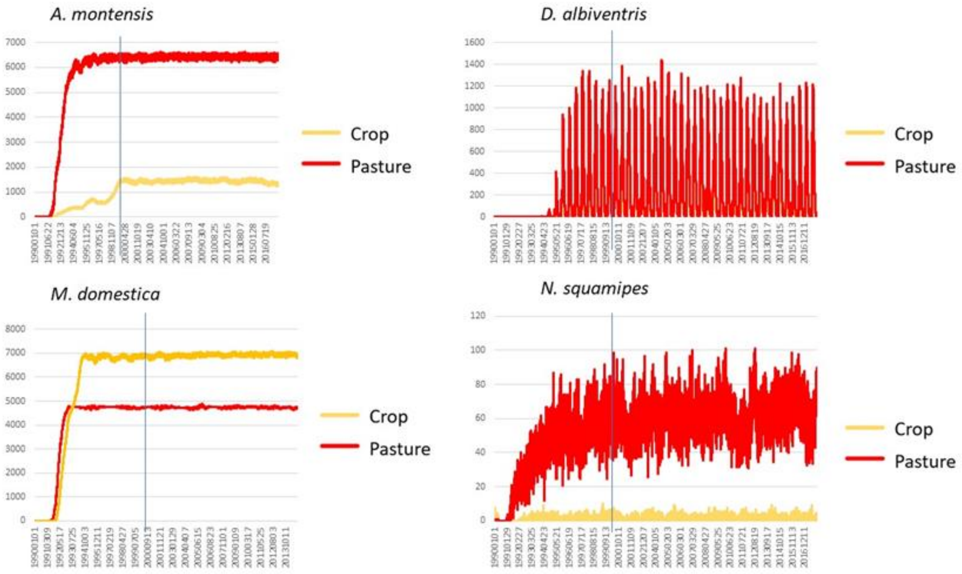
Figure 7.9. Number of agents throughout time into the matrix in the landscape with losses of savanna.



The graphs show in the axis each time step in the simulation and the axis y the number of agents of each species in the matrices.

Source: The author.

Figure 7.10. Number of agents throughout time into the matrix in the landscape with losses of grassland.



The graphs show in the axis each time step in the simulation and the axis y the number of agents of each species in the matrices. The model to M. domestica ran until 2014.
Source: The author.

7.4 Discussion

We did not observe the relaxation time or extinction debt in our modeling. Instead, we observed the stability of all the populations analyzed (*A. montensis, D. albiventris, M. domestica*, and *N. squamipes*) in the scenarios of losses of the forest, savanna, and grassland. We only observed a tendency of reduction of D*. albiventris* into the matrix. Kuussaari et al. (2009) explain that mammals should have many years of analysis after losses to observe changes in their population. We observed that our populations reached the first stability in the landscape after approximately nine years of simulation. Because of this, we have some possible explanations for our findings.

First, we observed that in our three scenarios the habitat loss occurred slowly throughout time (Figure 7.5), which could have impacted our results. The choice of those areas was taken to attempt the amount of habitat loss and the same range of habitat amount. Also, we brought the observation considering real data. However, if the changes in the landscape were abrupt this could bring a clearer observation of the impacts on the populations. This brings us to our first recommendation to further studies: to include and compare landscapes with abrupt losses of habitat and slow losses to observe the difference in the answer of populations. Here, we recommend at least 10 years of observation after habitat loss to observe the impact on small mammals, considering their life cycle and time to reach the first stability in our model (HALLEY; SGARDELI; TRIANTIS, 2014; KUUSSAARI et al., 2009).

Second, the losses of around 12% might not be relevant to the landscapes we analyzed, when all landscapes were around 40% of the habitat amount at the beginning of the simulations. This might be associated with the threshold to habitat loss, which means that beyond this threshold just generalist species are able to remain on the landscape. In Atlantic Rainforest, for example, the threshold for losses of small mammals is around 30% of native vegetation (PARDINI et al., 2010). Despite this number is not clear to the Cerrado, we would not observe the impacts of habitat loss if the landscape has already reached its threshold of habitat loss to small mammals.

Third, we did not measure the fragmentation evolution of the landscape in our simulations. According to Fahrig (2017), the different degrees of fragmentation in the same habitat amount can lead to different effects on biological populations. Also, the species-area relationship can be modulated by the corridors or stepping stones in the landscape (ROCHA et al., 2021; ROCHA; PASSAMANI; LOUZADA, 2011). The presence of corridors and steppingstones also can postpone the observation of the relaxation time (LITZA; DIEKMANN, 2020). The differences in the occupation of the Cerrado can lead to different degrees of fragmentation (ASSIS; ESCADA; AMARAL, 2021). This means that our three scenarios could result in different degrees of fragmentation affecting the responses of small mammals.

Another possible explanation for our findings is *that A. montensis, D. albiventris, M. domestica*, and *N. squamipes* can be found in disturbed places with a low percentage of habitat (ALMEIDA; TORQUETTI; TALAMONI, 2008; CÁCERES et al., 2010b; ERNEST; MARES, 1986; GOODIN et al., 2009). We expected fluctuations in the population patterns as a result of habitat loss, but even with high plasticity. The possibilities in the case of species with high plasticity can increase their abundance into patches because of the absence of competitors specialists, occupation of the matrix, or a minor reduction in the population size (PARDINI et al., 2010; UMETSU; PAUL METZGER; PARDINI, 2008). We did not observe any of those possibilities of fluctuations.

Considering the advances in the proposal of this model, we observed that the dynamic of the population was well designed since all the populations analyzed could reach an equilibrium in the landscape. The species could occupy the space, reproduce, and keep their population in all the scenarios. The absence in the literature of biological field data for all the species can be seen as a limitation to a good result and generalization of this model. Also, another limitation for the modelling is the high computional power demand, what can limitate the scenarios possible to simulate.

To improve the model power to simulate interactions to better address the hypothesis of time relaxation and extinction debt, we recommend simulating abrupt losses and longer time after habitat loss in accordance with Kuussaari et al. (2009). Our choices of using real spatial data in our simulations limited the possibility of the amplitude in the habitat losses and the habitat amount. A simulated landscape would bring the possibility of controlling the losses of habitat, the initial and final habitat amount, and how these losses occur. This would also bring the possibility to work with scenarios with different matrices and the combination of them in moderating the effects of habitat loss (ARROYO-RODRÍGUEZ et al., 2020).

7.5 Conclusion

Our model advances in the possibility to explore the effects of land cover changes on biological populations are free and will be available on the TerraME platform on Github. This possibility includes understanding the effects of habitat loss, habitat fragmentation, and matrix effects in the time relaxation and the extinction debt of biological populations. We found some limitations in using real spatial data in our study. Because of this, we would recommend further studies to select areas with controlled habitat amount and the type of matrix in the different scenarios and controlled fragmentation. We also would recommend keeping simulation for longer, 10 years at least for small mammals, to understand better the effects of habitat loss in long-term analyzes.

8 GENERAL DISCUSSION

This chapter discusses, in an integrated way, the core aspects of the results obtained in this thesis. The results in Chapter 2 presented the theoretical background that supported this thesis. Chapter 3 pointed out the impact of the anthropogenic land cover on the patterns of natural habitats in the Cerrado landscape considering both: habitat loss and fragmentation. Chapter 4 advances the knowledge of the role played by the conservation policies to protect natural habitats in the Cerrado. After knowing the landscape patterns, Chapter 5 advanced in the discussion on the best practices in defining scale in landscape ecology studies, specifically for small mammals, the group used in this study. After this, Chapter 6 explored how the small mammals' community from different habitat types answers to different anthropogenic land cover. And finally, Chapter 7 brings as a novelty the agent-based model to discuss the time response of population from different habitat types – forest, savanna, and grassland - to land cover changes, with the perspective of the relaxation time and extinction debt.

The main implications of Chapter 3 relate to the low density of the Cerrado patches in the frontier region of the Cerrado (mean 11,402 patches per 5km x 5km cell); the dominance of a single type of anthropic matrix, annual croplands, or pastures over extensive areas; Cerrado deforestation in Bahia also has a particular landscape pattern of natural vegetation loss, reducing large patches inside landscapes with initial and intermediate levels of fragmentation and inside landscapes with a heterogeneous matrix. It is already known by previous studies that the main losses of the Cerrado natural habitats are happening in the north of the biome (ALENCAR et al., 2020; DE OLIVEIRA et al., 2017). But we brought as a novelty the patterns of how these losses occur in terms of the anthropogenic cover occupation, the pattern of fragmentation as a process reducing the size of the patches. Our results in Chapter 3 reinforces the importance of the north of the Cerrado biome to protect its pristine areas because the concentration of large or continuous areas of natural habitat in the region is greater than in the central and south region of the biome (BARRETO et al., 2012; POLIZEL et al., 2021).

To better understand the patterns found in Chapter 3, Chapter 4 advanced in understanding how the main anthropogenic matrix found in the Cerrado biome, crop and pasture (SOUZA et al., 2020), affect the landscape patterns and how they relate to the policies of conservation. First, we could understand the impacts of crop and pasture on the landscape fragmentation and habitat amount, and we observed that landscapes dominated by crops have more impact in reducing habitat amount and the number of patches in the landscape. The impacts of habitat loss on biodiversity are widely known (MYERS et al., 2000b), but comparing landscapes with the same habitat amount, the reduction in the number of patches also has negative impacts on the biological community (FAHRIG, 2017, 2020). Our results show that the pattern found in landscapes dominated by crops has less habitat, and fewer patches with areas larger than landscapes dominate by pasture.

The second main implication of Chapter 4 is our finding that the majority of the natural habitats in the Cerrado biome are concentrated in Legal Reserves or the Brazilian Forest Code. Once the Legal Reserves are mainly concentrated in private lands (POLIZEL et al., 2021; ROSA, 2021), our results show the relevance of the Legal Reserves to the Cerrado conservation. It is also important to notice that Protected Areas are the more restrictive, and therefore more efficient in their protection, but protect only about 10% of the current area of forest, savanna, and grassland.

After understanding the patterns in the landscape, the next step was to establish the scale to study the small mammals' interactions with the landscape. Because of this, we did a review in Chapter 5 to understand how to best define scales and landscape representation in mammal studies. From our review, a total of 24 articles justified the choice of spatial scale. We identified three methods that authors used to justify the chosen extent: (1) based only on spatial characteristics,

(2) based on the relationship between species behavior and space, and (3) by testing the scale of effect. The argument most frequently used to justify the extent was the “scale of effect”. Based on this review, we recommended choosing the extent based on the scale of effect (JACKSON; FAHRIG, 2012). This means testing different scales and seeing in each scale the specie answer to the landscape. Our second recommendation is to choose the resolution based on the structures in the landscape that are used by the mammal group. This means choosing the resolution that can represent landscape structures that work as barriers or corridors to species. Last, choose heterogeneity according to the species' perception of the environment. This recommendation is special relevant considering that some species can use some matrices as habitat, or to move in different matrices with different degrees of percolation (PREVEDELLO; VIEIRA, 2010b).

After having defined the scale and understood the landscape patterns, we could verify the effects of anthropogenic land covers on the small mammal species. In Chapter 6 we presented how different types of anthropogenic land cover affect the small mammals in different habitat types. In opposition to the common finds in the literature that the matrix with a similar structure to the habitat is better for biological communities (EYCOTT et al., 2012), our results showed that the presence of the matrix is more like a disturbance than a habitat extension. This changes how to interpret the landscape and design optical landscapes for biological conservation (ARROYO-RODRÍGUEZ et al., 2020). Another recommendation to further studies is to verify the relationship between how the matrix quality is measured and not just biomass and structure (REIDER; DONNELLY; WATLING, 2018; RUFFELL; CLOUT; DIDHAM, 2017).

Finally, in Chapter 7, we built a model that brought the possibility to simulate the interaction of land cover changes throughout time and measure the time relaxation, or the time a population takes to reach stability after a disturbance, and the extinction debt. Even though we did not observe any changes after the habitat loss in any of the scenarios evaluated, we could observe that the populations were able to achieve stability in the landscape in all simulations. Our methodological choice of simulating a real landscape limited the options of choosing areas with abrupt habitat loss, which could make it possible to observe clearer the effects of the habitat loss. We also recommend further studies to keep the simulation for a longer time to observe the effects of time relaxation, in agreement with Kuussaari et al. (2009).

9 FINAL CONCLUSION

The objective of this thesis was to understand the effects of the land cover changes on the fauna of small mammals in the Brazilian Cerrado. To achieve this objective, we initiated by understanding how the land cover changes in Cerrado occur in the frontier of habitat loss. We continued studying the Cerrado landscape, the relationship of the natural habitat configuration in the landscape with the anthropogenic matrices, and how the conservation of the Cerrado natural habitats relates to conservation policies. Then, we studied how to define scale to small mammal studies. From this, we selected landscapes to study how different types of anthropogenic matrices affect the small mammal communities from different types of Cerrado natural habitats. Finally, we proposed a model to understand how the land cover changes affect the small mammal populations throughout time. In this chapter, there is a summary of the results for the questions we asked in this thesis, policy implications, and recommendations to further studies.

9.1 Summary of the answers to the research questions

In this section, we present the summary of the answers to the questions presented in this thesis.

a) *How does the deforestation process change the landscape structure (or landscape patterns) in the Brazilian Cerrado, and where do the losses of native Cerrado occur in the landscape context?*

The landscape changes in Cerrado increase the dominance of single matrices. We found an evident dominance of a single type of anthropic matrix, annual croplands, or pastures. Also, the losses of natural habitats reduce large patches inside landscapes with initial and intermediate levels of fragmentation and inside landscapes with a heterogeneous matrix.

b) Does the amount of Cerrado natural habitat differ in landscapes with a predominance of pasture vs. a predominance of crops?

We found that the loss of Cerrado's natural habitat is higher in landscapes dominated by crops than those dominated by pastures, which is an unexpected result. In fact, we expected the same impact on habitat loss in crops and agriculture because habitat protection policies in Brazil do not differ for these two major types of agriculture.

c) *Are the different types of Cerrado natural habitats - forest, savanna, and grassland - equally protected by the different policies for habitat protection in Brazil?*

Our results suggest there is little or no bias in the type of Cerrado´s natural habitat being protected by current habitat conservation policies. As a proportion of the current cover of the Cerrado natural habitats, there is a larger proportion of current forest than savanna or grassland under protection. Considering the mechanisms of conservation, Legal Reserves protect the highest proportion of the Cerrado natural habitats.

d) *Is the level of fragmentation of Cerrado natural habitat higher in landscapes with a predominance of pasture than in landscapes dominated by crops?*

Our analysis of habitat fragmentation per se relating to the type of agriculture suggests that crops have a larger impact on Cerrado biodiversity than pastures. For a given amount of natural habitat, the habitat in landscapes with a predominance of pasture is more fragmented than in landscapes with a predominance of crops. This means that in the same habitat amount, the landscape dominated by pasture has more and smaller patches than landscapes dominated by crops.

e) *How do mammal focused landscape-scale studies in Brazil deal with scale? Is there a common approach among mammalian landscape ecology studies in Brazil to define the scale and representation of* *landscapes?*

We found that the majority of studies in Brazil do not justify scale and, in general, there is not a common approach to it. From the papers that justified scale, we identified three ways that the authors used to justify their choice of spatial scale extent: (1) based solely on spatial characteristics, such as distance, to avoid spatial correlation among sample units; (2) based on the relationship between species behavior and space, such as dispersal or daily movement and home range; and (3) to test the scale of effect and experiment with different extent sizes to find the scale that the species best answers to the landscape. Three studies justified their choice of resolution, using as an argument the species' behavior, specifically movement or home range. We found that the choice to represent the landscape as either heterogeneous or a forested/non-forested environment was related to the guiding research questions. From this review, we could recommend a common approach to further studies.

f) Does matrix type affect the richness of small mammals in different Cerrado natural habitats?

The effects of surrounding land cover on small mammal species richness at sampling sites were weak. We found a positive coefficient for silviculture and pasture, stronger for the last one, inside forest habitat. For the savanna habitat, crops had the smallest negative coefficient of the three matrix types as predicted, but the difference among them was not large. For grassland habitat, the coefficient for crops was positive and the largest of the coefficients for the three matrix types. We observed a strong positive effect of the percentage of pasture on species richness in forest sites. But we did not observe any effects of the matrix on species richness in savanna and grassland sites.

g) Does matrix type change the species composition of small mammals in different Cerrado natural habitats?

The matrix type changes the species composition of small mammals in different Cerrado natural habitats. Irrespective of the habitat type where the sample was taken, there are more mammal forest species in sites surrounded by more pasture and there are fewer forest species in sites surrounded by more silviculture. The effect of crops in the matrix on forest species depends on where the small mammals were sampled. There are fewer savanna/grassland species in savanna sites surrounded by more savanna, but there are more savanna/grassland species in forest sites surrounded by more forest and in grassland sites surrounded by more grassland. There are more savanna/grassland species in forest sites and savanna sites surrounded by more pasture. There are more savanna/grassland species in savanna sites and grassland sites surrounded by more silviculture.

h) *How are relaxation time and the extinction debt observed in the small mammals' community?*

It was not possible to observe relaxation time or the extinction debt in the simulations. Instead, we observed the stability of all the populations analyzed (A*. montensis, D. albiventris, M. domestica,* and *N. squamipes*) in the scenarios of losses of forest, savanna, and grassland.

9.2 Implications

Based on the results, we indicated the following implications:

- The need to preserve the few contiguous fragments of this biome that have the function of preserving its natural processes (Chapter 3).
- The development of policies to protect the Cerrado natural habitats for croplands and pasturelands (Chapter 4).
- It is necessary to keep the Legal Reserve in the Brazilian Forest Code because most of the current natural habitat is under its protection (Chapter 4).

- To consider the best scale to analyze the effects of landscape, it is necessary to observe the elements of the landscape that affect biological responses (Chapter 5).
- To represent the components of the landscape the biological processes should be used as a guide to define spatial scale and representation (Chapter 5).
- It is important of considering the matrix type to design a more conservation-friendly landscape not only to increase permeability but to consider the impacts of the matrix type on natural communities' composition (Chapter 6).
- The ABM brings the possibility to understand long-term interactions between small mammal populations and landscape changes (Chapter 7).

9.3 Future work

This thesis has advanced the knowledge of the relationship between land cover changes in the Cerrado, the role played by the policies in the conservation of this biome, and how small mammals answer to different types of matrices and to habitat loss throughout time. But we also have some recommendations to further investigations:

- To investigate more deeply the relationship between matrix structure and matrix resources.
- To study the impacts of different types of matrices on species or communities within non-forest environments.
- To select areas with controlled habitat amount and the type of matrix in the different scenarios and controlled fragmentation.
- Longer simulations, 10 years at least to small mammals, to understand better the effects of habitat loss in long-term analyses.

- To study scenarios with abrupt habitat loss to observe clearer the impacts of habitat loss in the small mammal populations.

REFERENCES

ALENCAR, A. et al. Mapping three decades of changes in the brazilian Savanna native vegetation using Landsat data processed in the Google Earth Engine platform. **Remote Sensing**, v. 12, n. 6, p. 924, 2020.

GARDNER, A. L. (Ed.). **Mammals of South America, 1: marsupials, xenarthrans, shrews, and bats**. [S.l.]: University of Chicago Press, 2008.

ALHO, C. J. R.; PEREIRA, L. A.; PAULA, A. C. Patterns of habitat utilization by small mammal populations in Cerrado biome of central Brazil. **Mammalia**, v. 50, n. 4, p. 447– 460, 1986.

ALLEN, T. F. H.; HOEKSTRA, T. W. The confusion between scale-defined levels and conventional levels of organization in ecology. **Journal of Vegetation Science**, v. 1, n. 1, p. 5–12, 1990.

ALMEIDA, A. J. D.; TORQUETTI, C. G.; TALAMONI, S. A. by neotropical marsupial Use of space b y neotr opical mar supial Didelphis albiventris (Didelphimor phia : Didelphidae) in an urban f or est fr agment (Didelphimorphia : for orest fragment. **Revista Brasileira de Zoologia**, v. 25, n. 1976, p. 214–219, 2008.

ARROYO-RODRÍGUEZ, V. et al. Designing optimal human-modified landscapes for forest biodiversity conservation. **Ecology Letters**, v. 23, n. 9, p. 1404–1420, 2020.

ASSIS, T. O. et al. Use of forest fragments and agricultural matrices by small mammals in southeastern Brazil. **Mastozoología Neotropical**, v. 27, n. 1, p. 017–022, 2020.

ASSIS, T. O. et al. Scale and representation of landscapes in mammal studies in Brazil. **Acta Oecologica**, v. 114, p. 103817, 2022.

ASSIS, T. O.; ESCADA, M. I. S.; AMARAL, S. Effects of deforestation over the Cerrado landscape: a study in the Bahia frontier. **Land**, v. 10, n. 4, p. 352, 2021.

AUGUST, P. V. The role of habitat complexity and heterogeneity in sStructuring tropical mammal communitie. **Ecological Society of America**, v. 64, n. 6, p. 1495–1507, 1983.

BARRETO, L. et al. The impact of soybean expansion on mammal and bird, in the Balsas region, north Brasilian Cerrado. **Journal for Nature Conservation**,

v. 20, n. 6, p. 374– 383, 2012.

BATLLE-BAYER, L.; BATJES, N. H.; BINDRABAN, P. S. Changes in organic carbon stocks upon land use conversion in the brazilian Cerrado: a review. **Agriculture, Ecosystems and Environment**, v. 137, n. 1–2, p. 47–58, 2010.

BERTASSONI, A. et al. Land-use changes and the expansion of biofuel crops threaten the giant anteater in southeastern Brazil. **Journal of Mammalogy**, v. 100, n. 2, p. 435– 444, 2019.

BEUCHLE, R. et al. Land cover changes in the brazilian Cerrado and Caatinga biomes from 1990 to 2010 based on a systematic remote sensing sampling approach. **Applied Geography**, v. 58, p. 116–127, 2015.

BOESING, A. L.; NICHOLS, E.; METZGER, J. P. Biodiversity extinction thresholds are modulated by matrix type. **Ecography**, v. 41, n. 9, p. 1520–1533, 2018.

BOLFE, É. L. et al. Matopiba em crescimento agrícola: aspectos territoriais e socioeconômicos. **Revista de Política Agrícola**, v. 24, n. 4, p. 38–62, 2016.

BONVICINO, C. R.; LEMOS, B.; WEKSLER, M. Small mammals of Chapada dos Veadeiros National Park (Cerrado of Central Brazil): ecologic, karyologic, and taxonomic considerations. **Brazilian Journal of Biology**, v. 65, n. 3, p. 395–406, ago. 2005.

BOSCOLO, D. et al. Importance of interhabitat gaps and stepping-stones for lesser woodcreepers (Xiphorhynchus fuscus) in the Atlantic Forest , Brazil. **Ibis**, v. 40, n. 3, p. 273–276, 2008.

BRADY, M. J. et al. Matrix is important for mammals in landscapes with small amounts of native forest habitat. **Landscape Ecology**, v. 26, n. 5, p. 617–628, 2011.

BRASIL. MINISTÉRIO DO MEIO AMBIENTE. Lista nacional oficial de espécies da fauna ameaçada de extinção. Portaria n^{o} 444, de 17 de dezembro de 2014. Ministério do Meio Ambiente. **Diário Oficial da União**, v. 245, n. 1, p. 121–126, 2014.

BRETT, J. G. Is landscape connectivity a dependent or independent variable? **Landscape Ecology**, v. 18, n. 7, p. 687–699, 2003.

BRITO, A.; VALERIANO, D. D. M.; FERRI, C.; SCOLASTRICI, A.; SESTINI, M. **Metodologia da deteccao do desmatamento no bioma Cerado: mapeamento de areas antropizadas com imagens de media resolucao espacial**. São José dos Campos: FUNCATE, 2018.

BRONDIZIO, E. S. et al. **Global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services**. [S.l.]: IPBES, 2019.

BUENO, C.; FAUSTINO, M. T.; FREITAS, S. R. Influence of landscape characteristics on capybara road-kill on highway BR-040, Southeastern Brazil. **Oecologia Australis**, v. 17, n. 2, p. 130–137, 2013.

CÁCERES, N. C. et al. Mammals in a fragmented savanna landscape in south-western Brazil. **Journal of Natural History**, v. 44, n. 7–8, p. 491–512, 2010a.

CÁCERES, N. C. et al. Mammals in a fragmented savanna landscape in south-western Brazil. **Journal of Natural History**, v. 44, n. 7–8, p. 491–512, 2010b.

CÁCERES, N. C.; MONTEIRO-FILHO, E. L. A. Food habits, home range and activity of didelphis aurita (Mammalia, Marsupialia) in a forest fragment of southern Brazil. **Studies on Neotropical Fauna and Environment**, v. 36, n. 2, p. 85–92, 2001.

CAMARGO, A. C. L. et al. Fire affects the occurrence of small mammals at distinct spatial scales in a neotropical savanna. **European Journal of Wildlife Research**, v. 64, 2018.

CAMARGO, N. F. DE et al. Frugivoria e potencial dispersão de sementes pelo marsupial Gracilinanus agilis (Didelphidae: Didelphimorphia) em áreas de Cerrado no Brasil central. **Acta Botanica Brasilica**, v. 25, n. 3, p. 646–656, 2011.

CARMIGNOTTO, A. P.; BEZERRA, A. M. R.; RODRIGUES, F. H. G. Nonvolant small mammals from a southwestern area of Brazilian Cerrado: diversity, habitat use, seasonality, and biogeography. **Therya**, v. 5, n. 2, p. 535–558, 2014.

CARVALHO, F. M. V.; DE MARCO, P.; FERREIRA, L. G. The Cerrado into-pieces: Habitat fragmentation as a function of landscape use in the savannas of central Brazil. **Biological Conservation**, v. 142, n. 7, p. 1392–1403, jul. 2009a.

CARVALHO, F. M. V.; DE MARCO, P.; FERREIRA, L. G. The Cerrado into-pieces: Habitat fragmentation as a function of landscape use in the savannas of central Brazil. **Biological Conservation**, v. 142, n. 7, p. 1392–1403, jul. 2009b.

CAVA, M. G. B. et al. Abandoned pastures cannot spontaneously recover the attributes of old-growth savannas. **Journal of Applied Ecology**, v. 55, n. 3, p. 1164–1172, 2018.

COELHO, A. J. P. et al. Effects of anthropogenic disturbances on biodiversity and biomass stock of Cerrado, the Brazilian savanna. **Biodiversity and Conservation**, v. 29, n. 11, p. 3151–3168, 2020.

COSTA, L. P. et al. Mammal conservation in Brazil. **Conservation Biology**, v. 19, n. 3, p. 672–679, jun. 2005.

CURI, N. H. A. et al. Risk factors for gastrointestinal parasite infections of dogs living around protected areas of the Atlantic Forest: implications for human and wildlife health. **Brazilian Journal of Biology**, v. 77, n. 2, p. 388–395, 2017.

DA ROSA, C. A. et al. Alien terrestrial mammals in Brazil: current status and management. **Biological Invasions**, v. 19, n. 7, p. 2101–2123, 2017.

D'ANDREA, P. S. et al. Ecology of small mammals in a Brazilian rural area. **Revista Brasileira de Zoologia**, v. 16, n. 3, p. 611–620, 1999.

DE OLIVEIRA, S. N. et al. Landscape-fragmentation change due to recent agricultural expansion in the Brazilian Savanna, Western Bahia, Brazil. **Regional Environmental Change**, v. 17, n. 2, p. 411–423, 2017.

DELCIELLOS, A. C. et al. Habitat fragmentation affects individual condition: evidence from small mammals of the Brazilian Atlantic Forest. **Journal of Mammalogy**, v. 99, n. 4, p. 936–945, 2018.

DINIZ-FILHO, J. et al. Spatial patterns of terrestrial vertebrate species richness in the brazilian Cerrado. **Zoological Studies**, v. 47, n. 2, p. 146–157, 2008.

DIRZO, R. et al. Defaunation in the Antrhopocene. **Science**, v. 401, n. 6195, p. 401–406, 2014.

DOBROVOLSKI, R. et al. Agricultural expansion and the fate of global conservation priorities. **Biodiversity and Conservation**, v. 20, n. 11, p. 2445–2459, 2011.

DOHERTY, T. S.; DRISCOLL, D. A. Coupling movement and landscape ecology for animal conservation in production landscapes. **Proceedings of the Royal Society B: Biological Sciences**, v. 285, n. 1870, p. 20172272, 2018.

DOTTA, G.; VERDADE, L. M. Medium to large-sized mammals in agricultural landscapes of south-eastern Brazil. **Mammalia**, v. 75, n. 4, p. 345–352, 2011a.

DOTTA, G.; VERDADE, L. M. Medium to large-sized mammals in agricultural landscapes of south-eastern Brazil. **Mammalia**, v. 75, n. 4, p. 345–352, 2011b.

DRAY, S. et al. Community ecology in the age of multivariate spatial analysis. **Ecological Monographs**, v. 82, n. 3, p. 257–275, 2012.

DRISCOLL, D. A. et al. Conceptual domain of the matrix in fragmented landscapes.
Trends in Ecology and Evolution, v. 28, n. 10, p. 605–613, 2013.

ERNEST, K. A.; MARES, M. A. Ecology of *Nectomys squamipes*, the Neotropical water rat, in central Brazil: home range, habitat selection, reproduction and behaviour. **Journal of Zoology**, v. 210, n. 4, p. 599–612, 1986.

ESPÍRITO-SANTO, M. M. et al. Understanding patterns of land-cover change in the Brazilian Cerrado from 2000 to 2015. **Philosophical Transactions of the Royal Society B: Biological Sciences**, v. 371, n. 1703, p. 20150435, 2016.

EWERS, R. M.; DIDHAM, R. K. Confounding factors in the detection of species responses to habitat fragmentation. **Biological reviews of the Cambridge Philosophical Society**, v. 81, n. 1, p. 117–42, 2006.

EYCOTT, A. E. et al. A meta-analysis on the impact of different matrix structures on species movement rates. **Landscape Ecology**, v. 27, n. 9, p. 1263–1278, 2012.

FAHRIG, L. Effects of habitat fragmentation on biodiversity. **Annual Review of Ecology, Evolution, and Systematics**, v. 34, n. 1, p. 487–515, 2003.

FAHRIG, L. Rethinking patch size and isolation effects: the habitat amount hypothesis. **Journal of Biogeography**, v. 40, n. 9, p. 1649–1663, 2013.

FAHRIG, L. Ecological responses to habitat fragmentation per se. **Annual Review of Ecology, Evolution, and Systematics**, v. 48, n. 1, p. 1–23, 2017.

FAHRIG, L. Habitat fragmentation: a long and tangled tale. **Global Ecology and Biogeography**, v. 28, n. 1, p. 33–41, 2019.

FAHRIG, L. et al. Is habitat fragmentation bad for biodiversity? **Biological Conservation**, v. 230, p. 179–186, 2019.

FAHRIG, L. Why do several small patches hold more species than few large patches? **Global Ecology and Biogeography**, v. 29, n. 4, p. 615–628, 2020.

FARIA, D. et al. Implications of habitat loss on seed predation and early recruitment of a keystone palm in anthropogenic landscapes in the brazilian atlantic rainforest Leiza Aparecida S. S. Soares. **PLoS ONE**, v. 10, n. 7, p. 1–14, 2015.

FIALHO, M. Y. G.; CERBONCINI, R. A. S.; PASSAMANI, M. Can vegetation corridors support a small mammal community similar to that found within forest fragments? A case study in southeastern Brazil. **Studies on Neotropical Fauna and Environment**, v. 52, n. 1, p. 64–67, 2017.

FISCHER, C.; THIES, C.; TSCHARNTKE, T. Small mammals in agricultural landscapes: opposing responses to farming practices and landscape complexity. **Biological Conservation**, v. 144, n. 3, p. 1130–1136, 2011.

FLETCHER, R. J. et al. Is habitat fragmentation good for biodiversity? **Biological Conservation**, v. 226, n. July, p. 9–15, 2018.

FORERO-MEDINA, G.; VIEIRA, M. V. Perception of a fragmented landscape by neotropical marsupials: effects of body mass and environmental variables. **Journal of Tropical Ecology**, v. 25, n. 1, p. 53–62, 2009.

FORMAN, R. T. **Land mosaics: the ecology of landscapes and regions**. [S.l.]: Cambridge University Press, 1995.

FORMAN, R. T. T.; GODRON, M. Components ecology landscape structural. **Sciences- New York**, v. 31, n. 10, p. 733–740, 2008.

FRANÇOSO, R. D. et al. Habitat loss and the effectiveness of protected areas in the Cerrado biodiversity hotspot. **Natureza e Conservacao**, v. 13, n. 1, p. 35–40, 2015.

FREITAS, S. R. et al. A model of road effect using line integrals and a test of the performance of two new road indices using the distribution of small mammals in an Atlantic Forest landscape. **Ecological Modelling**, v. 247, p. 64–70, 2012.

FURLEY, P. A.; RATTER, J. A. Soil resources and plant communities of the central brazilian Cerrado and their development. **Journal of Biogeography**, v. 15, n. 1, p. 97, 1988.

GANEM, R. S.; DRUMMOND, J. A.; FRANCO, J. L. DE A. Conservation polices and control of habitat fragmentation in the Brazilian Cerrado biome. **Ambiente & Sociedade**, v. 16, n. 3, p. 99–118, 2013.

GASCON, C. et al. Matrix habitat and species richness in tropical forest remnants. **Journal of Biogeography**, v. 91, p. 223–229, 1999.

GENTILE, R.; CERQUEIRA, R. Movement patterns of five species of sSmall mammals in a brazilian Restinga. **Journal of Tropical Ecology**, v. 11, n. 4, p. 671–677, 1995.

GIBSON, C. C.; OSTROM, E.; AHN, T. K. The concept of scale and the human dimensions of global change: a survey. **Ecological Economics**, v. 32, n. 2, p. 217–239, 2000.

GILBERT, G. E. **Linear mixed models: a practical guide using statistical software**. [S.l]: CRC Press, 2014.

GOMES, J. B. V. et al. Análise de componentes principais de atributos físicos, químicos e mineralógicos de solos do bioma cerrado. **Revista Brasileira de Ciência do Solo**, v. 28, n. 1, p. 137–153, 2004.

GOODIN, D. G. et al. Microhabitat characteristics of *Akodon montensis*, a reservoir for hantavirus, and hantaviral seroprevalence in an Atlantic forest site in eastern Paraguay. **Journal of Vector Ecology**, v. 34, n. 1, p. 104–113, 2009.

GRIMM, V. et al. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. **Science**, v. 310, n. 5750, p. 987–991, 2005a.

GRIMM, V. et al. Importance of buffer mechanisms for population viability analysis. **Conservation Biology**, v. 19, n. 2, p. 578–580, 2005b.

GRIMM, V. et al. The ODD protocol: a review and first update. **Ecological Modelling**, v. 221, n. 23, p. 2760–2768, 2010.

HAILA, Y. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. **Ecological Applications**, v. 12, n. 2, p. 321–334, 2002.

HALLEY, J. M.; SGARDELI, V.; TRIANTIS, K. A. Extinction debt and the species–area relationship: a neutral perspective. **Global Ecology and Biogeography**, v. 23, n. 1, p. 113–123, 2014.

HANNIBAL, W. et al. Multi-scale approach to disentangle the small mammal composition in a fragmented landscape in central Brazil. **Journal of Mammalogy**, v. 99, n. 6, p. 1455–1464, 2018a.

HANNIBAL, W. et al. Multi-scale approach to disentangle the small mammal composition in a fragmented landscape in central Brazil. **Journal of Mammalogy**, v. 99, n. 6, p. 1455–1464, 2018b.

HARDT, E. et al. Does certification improve biodiversity conservation in Brazilian coffee farms? **Forest Ecology and Management**, v. 357, p. 181–194, 2015.

HENDGES, C. D. et al. Landscape attributes as drivers of the geographical variation in density of Sapajus nigritus Kerr, 1792, a primate endemic to the Atlantic Forest. **Acta Oecologica**, v. 84, p. 57–63, 2017.

HENGEVELD, R;. MACARTHUR, R.H.; WEILSON, E.O. The theory of island biogeography. **Acta Biotheoretica**, v. 50, n. 2, p. 133–136, 1 jun. 2002.

HENRIQUES, R. P. B. et al. A simple graphical model of small mammal succession after fire in the Brazilian cerrado. **Mammalia**, v. 70, n. 3–4, p. 226–230, 2006.

HONORATO, R. et al. The effects of habitat availability and quality on small mammals abundance in the Brazilian Atlantic Forest. **Natureza e Conservacao**, v. 13, n. 2, p. 133– 138, 2015.

HUBBELL, S. P. **The unified netural theory of biodiversity and biogeopraphy.** Princeton: Princeton University Press, 2011.

INSTITUTO BRASILEIRO DE GEOGRAFIA E ESTATÍSTICA (IBGE). **Características gerais dos indígenas: resultado do universo**. Rio de Janeiro: IBGE, 2010.

JACKSON, H. B.; FAHRIG, L. What size is a biologically relevant landscape? **Landscape Ecology**, v. 27, n. 7, p. 929–941, 2012.

JACKSON, H. B.; FAHRIG, L. Are ecologists conducting research at the optimal scale? **Global Ecology and Biogeography**, v. 24, n. 1, p. 52–63, 2015.

KLINK, C. A.; MACHADO, R. B. Conservation of the brazilian Cerrado. **Conservation Biology**, v. 19, n. 3, p. 707–713, 2005.

KÖRTING, T. S.; GARCIA FONSECA, L. M.; CÂMARA, G. GeoDMA—Geographic data mining analyst. **Computers & Geosciences**, v. 57, p. 133–145, 2013.

KUUSSAARI, M. et al. Extinction debt: a challenge for biodiversity conservation. **Trends in Ecology and Evolution**, v. 24, n. 10, p. 564–571, 2009.

LAHSEN, M. Seductive simulations? uncertainty distribution around climate models. **Social Studies of Science**, v. 35, n. 6, p. 895–922, 2005.

LAHSEN, M.; BUSTAMANTE, M. M. C.; DALLA-NORA, E. L. Undervaluing and overexploiting the brazilian Cerrado at our peril. **Environment: Science and Policy for Sustainable Development**, v. 58, n. 6, p. 4–15, 2016.

LAURANCE, W. F.; SAYER, J.; CASSMAN, K. G. Agricultural expansion and its impactos on tropical nature. **Trends in Ecology & Evolution**, v. 29, n. 2, p. 107–116, 2014.

LEHMANN, C. E. R.; PARR, C. L. Tropical grassy biomes: linking ecology, human use and conservation. **Philosophical Transactions of the Royal Society B: Biological Sciences**, v. 371, n. 1703, p. 20160329, 2016.

LIRA, P. K. et al. Evaluating the legacy of landscape history: extinction debt and species credit in bird and small mammal assemblages in the Brazilian Atlantic Forest. **Journal of Applied Ecology**, v. 49, n. 6, p. 1325–1333, 2012.

LITZA, K.; DIEKMANN, M. The effect of hedgerow density on habitat quality distorts species-area relationships and the analysis of extinction debts in hedgerows. **Landscape Ecology**, v. 35, n. 5, p. 1187–1198, 2020.

LYRA-JORGE, M. C. et al. Influence of multi-scale landscape structure on the occurrence of carnivorous mammals in a human-modified savanna, Brazil. **European Journal of Wildlife Research**, v. 56, n. 3, p. 359–368, 2010.

MARTIN, A. E. The spatial scale of a species' response to the landscape context depends on which biological response you measure. **Current Landscape Ecology Reports**, v. 3, n. 1, p. 23–33, 2018.

MARTIN, A. E.; FAHRIG, L. Reconciling contradictory relationships between mobility and extinction risk in human-altered landscapes. **Functional Ecology**,

v. 30, n. 9, p. 1558–1567, 2016.

MARTINELLI, L. A. et al. Agriculture in Brazil: impacts, costs, and opportunities for a sustainable future. **Current Opinion in Environmental Sustainability**, v. 2, n. 5–6, p. 431–438, 2010.

MATTHEWS, R. B. et al. Agent-based land-use models: a review of applications. **Landscape Ecology**, v. 22, n. 10, p. 1447–1459, 1 dez. 2007.

MAZOR, T. et al. Global mismatch of policy and research on drivers of biodiversity loss. **Nature Ecology and Evolution**, v. 2, n. 7, p. 1071–1074, 2018.

MEENTEMEYER, V. Geographical perspectives of space, time, and scale. **Landscape Ecology**, v. 3, n. 3–4, p. 163–173, 1989.

MELO, G. L. et al. Testing the habitat amount hypothesis for South American small mammals. **Biological Conservation**, v. 209, p. 304–314, 2017a.

MELO, G. L. et al. Testing the habitat amount hypothesis for South American small mammals. **Biological Conservation**, v. 209, p. 304–314, 2017b.

MENDES, P.; DE MARCO, P. Bat species vulnerability in Cerrado: integrating climatic suitability with sensitivity to land-use changes. **Environmental Conservation**, v. 45, n. 1, p. 67–74, 2018.

MENDONÇA, A. F. et al. Effects of an extensive fire on arboreal small mammal populations in a neotropical savanna woodland. **Journal of Mammalogy**, v. 96, n. 2, p. 368–379, 2015.

MESQUITA, A. O.; PASSAMANI, M. Composition and abundance of small mammal communities in forest fragments and vegetation corridors in Southern Minas Gerais, Brazil. **Revista de Biologia Tropical**, v. 60, n. 3, p. 1335–1343, 2012.

METZGER, J.; DDCAMPS, H. FORUM The structural connectivity threshold : an hypothesis in conservation biology at the landscape scale Connectivity characterizes the capacity of a landscape to facilitate or impede movement among resource patches (. v. 18, n. 1, p. 1–12, 1997.

METZGER, J. P. Conservation issues in the Brazilian Atlantic forest. **Biological Conservation**, v. 142, n. 6, p. 1138–1140, 2009.

METZGER, J. P.; NEOTROPICA, B. O QUE É ECOLOGIA DE PAISAGENS ?

Landscape Ecology, p. 1–9, 2001.

MIGUEL, P. H. et al. Habitat amount partially affects physiological condition and stress level in Neotropical fruit-eating bats. **Comparative Biochemistry and Physiology -Part A : Molecular and Integrative Physiology**, v. 237, p. 110537, 2019.

MILLENNIUM ECOSYSTEM ASSESSMENT (PROGRAM) (ED.). **Ecosystems and human well-being: synthesis**. Washington, DC: Island Press, 2005.

MILLER-RUSHING, A. J. et al. How does habitat fragmentation affect biodiversity? A controversial question at the core of conservation biology. **Biological Conservation**, v. 232, p. 271–273, 2019.

MORAES, A. M. et al. Landscape resistance influences effective dispersal of endangered golden lion tamarins within the Atlantic Forest. **Biological Conservation**, v. 224, , p. 178–187, 2018.

MORAGA, A.; MARTIN, A.; FAHRIG, L. The scale of effect of landscape context varies with the species' response variable measured. **Landscape Ecology**, v. 34, 1 abr. 2019.

MYERS, N. et al. Biodiversity hotspots for conservation priorities. **Nature**, v. 403, n. 6772, p. 853–8, 2000a.

MYERS, N. et al. Biodiversity hotspots for conservation priorities. **Nature**, v. 403, n. 6772, p. 853–8, 2000b.

NOGUEIRA, J. M. P. et al. Spatial pattern of the seasonal drought/burned area relationship across brazilian biomes: sensitivity to drought metrics and global remote-sensing fire products. **Climate**, v. 5, n. 2, p. 42, 2017.

OLIFIERS, N.; GENTILE, R.; FISZON, J. T. Relation between small-mammal species composition and anthropic variables in the Brazilian Atlantic Forest. **Brazilian Journal of Biology**, v. 65, n. 3, p. 495–501, ago. 2005.

PAGLIA, A. P. et al. **Lista anotada dos mamíferos do Brasil**. [s.l: s.n.]. v. 4

PALMEIRIM, A. F. et al. Small mammal responses to Amazonian forest islands are modulated by their forest dependence. **Oecologia**, v. 187, n. 1, p. 191–204, 2018.

PARDINI, R. et al. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. **Biological Conservation**, v. 124, n. 2, p. 253–266, jul. 2005.

PARDINI, R. et al. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. **PloS one**, v. 5, n. 10, p. e13666, jan. 2010.

PARKER, D. C. et al. Multi-agent systems for the simulation of land-use and land-cover change: a review. **Annals of the Association of American Geographers**, v. 93, n. 2, p. 314–337, 2003.

PARRY, L.; BARLOW, J.; PERES, C. A. Allocation of hunting effort by Amazonian smallholders: Implications for conserving wildlife in mixed-use landscapes. **Biological Conservation**, v. 142, n. 8, p. 1777–1786, 2009.

PATTON, J. L.; PARDIÑAS, U. F.J.; D'ELÍA, G. (Ed.). **Mammals of South America, volume 2: rodents**. University of Chicago Press, 2015.

PHALAN, B. et al. Crop expansion and conservation priorities in tropical countries. **PLoS ONE**, v. 8, n. 1, 2013.

PIMENTA, N. C. et al. The return of giant otter to the Baniwa Landscape: a multi-scale approach to species recovery in the middle Içana River, Northwest Amazonia, Brazil. **Biological Conservation**, v. 224, p. 318–326, 2018.

PIRES FERNANDEZ, F. A. S., A. S. Use of space by the marsupial Micoreus demerarae in small Atlantic Forest fragments in south-eastern Brazil. **Journal of Tropical Ecology**, v. 15, p. 279–290, 1999.

POLIZEL, S. P. et al. Analysing the dynamics of land use in the context of current conservation policies and land tenure in the Cerrado – MATOPIBA region (Brazil). **Land Use Policy**, v. 109, p. 105713, 2021.

PREVEDELLO, J. A.; VIEIRA, M. V. Plantation rows as dispersal routes: a test with didelphid marsupials in the Atlantic Forest, Brazil. **Biological Conservation**, v. 143, n. 1, p. 131–135, jan. 2010a.

PREVEDELLO, J. A.; FORERO-MEDINA, G.; VIEIRA, M. V. Movement behaviour within and beyond perceptual ranges in three small mammals: effects of matrix type and body mass. **The Journal of Animal Ecology**, v. 79,

n. 6, p. 1315–23, nov. 2010.

PREVEDELLO, J. A.; VIEIRA, M. V. Does the type of matrix matter? A quantitative review of the evidence. **Biodiversity and Conservation**, v. 19, n. 5, p. 1205–1223, 2010b.

PÜTTKER, T. et al. Responses of five small mammal species to micro-scale variations in vegetation structure in secondary Atlantic Forest remnants , Brazil. **BMC Ecology**, v. 10, p. 1–10, 2008.

PÜTTKER, T. et al. Immigration rates in fragmented landscapes--empirical evidence for the importance of habitat amount for species persistence. **PloS one**, v. 6, n. 11, p. e27963, 2011.

PÜTTKER, T. et al. Habitat specialization interacts with habitat amount to determine dispersal success of rodents in fragmented landscapes. **Journal of Mammalogy**, v. 94, n. 3, p. 714–726, 2013.

PÜTTKER, T. et al. Indirect effects of habitat loss via habitat fragmentation: a cross- taxa analysis of forest-dependent species. **Biological Conservation**, v. 241, p. 108368, 2020.

PÜTTKER, T.; MEYER-LUCHT, Y.; SOMMER, S. Fragmentation effects on population density of three rodent species in secondary Atlantic Rainforest, Brazil. **Studies on Neotropical Fauna and Environment**, v. 43, n. 1, p. 11–18, 2008.

RAMOS PEREIRA, M. et al. Structure of small mammal assemblages across flooded and unflooded gallery forests of the Amazonia-Cerrado ecotone. **Biotropica**, v. 45, n. 4, p. 489–496, 2013.

RATTER, J. A.; RIBEIRO, J. F.; BRIDGEWATER, S. The brazilian Cerrado vegetation and threats to its biodiverisity. **Annals of Botany**, v. 80, p. 223–230, 1997a.

RATTER, J. A.; RIBEIRO, J. F.; BRIDGEWATER, S. The brazilian Cerrado vegetation and threats to its biodiverisity. **Annals of Botany**, v. 80, p. 223–230, 1997b.

REATTO, A., CORREIA, J.R. & SPERA, S. T. **Solos do bioma Cerrado: aspectos pedológicos.** [s.l: s.n.].

REGOLIN, A. L. et al. Forest cover influences occurrence of mammalian carnivores within Brazilian Atlantic Forest. **Journal of Mammalogy**, v. 98, n. 6, p. 1721–1731, 2017.

REIDER, I.; DONNELLY, M.; WATLING, J. The influence of matrix quality on species richness in remnant forest. **Landscape Ecology**, v. 33, 1 jul. 2018.

RIBEIRO, K. T.; FREITAS, L. Impactos potenciais das alterações no Código Florestal sobre a vegetação de campos rupestres e campos de altitude. **Biota Neotropica**, v. 10, n. 4,
p. 239–246, 2010a.

RIBEIRO, K. T.; FREITAS, L. Impactos potenciais das alterações no Código Florestal sobre a vegetação de campos rupestres e campos de altitude. **Biota Neotropica**, v. 10, n. 4, p. 239–246, 2010b.

RIBEIRO, M. C. et al. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. **Biological Conservation**, v. 142, n. 6, p. 1141–1153, 2009.

ROCHA, É. G. DA et al. Dispersal movement through fragmented landscapes: the role of stepping stones and perceptual range. **Landscape Ecology**, v. 36, n. 11, p. 3249– 3267, 2021.

ROCHA, E. C. et al. Effects of habitat fragmentation on the persistence of medium and large mammal species in the Brazilian Savanna of Goiás State. **Biota Neotropica**, v. 18, n. 3, 2018.

ROCHA, M. F.; PASSAMANI, M.; LOUZADA, J. A small mammal community in a forest fragment, vegetation corridor and coffee matrix system in the Brazilian Atlantic forest. **PloS one**, v. 6, n. 8, p. e23312, 2011.

ROSA, C. A. Savanna for sale: is there hope for neotropical biodiversity on private, Brazilian properties? **Animal Conservation**, v. 24, n. 1, p. 1–2, 2021.

RUFFELL, J.; CLOUT, M. N.; DIDHAM, R. K. The matrix matters, but how should we manage it? Estimating the amount of high-quality matrix required to maintain biodiversity in fragmented landscapes. **Ecography**, v. 40, n. 1, p. 171–178, 2017.

SCARAMUZZA, C. A. D. M. et al. Land-Use and Land-Cover mapping of the Brazilian Cerrado bases mainly on Landsat-8 Satellite Images. **Revista Brasileira de Cartografia**, v. 69, n. 6, p. 1041–1051, 2018.

SCARAMUZZA, C. A. DE M. et al. LAND-USE AND LAND-COVER MAPPING

OF THE BRAZILIAN CERRADO BASED MAINLY ON LANDSAT-8 SATELLITE IMAGES Mapeamento de Uso e Cobertura de Terras do Cerrado com Base Principalmente em Imagens do Satélite Landsat-8 Ministério do Meio Ambiente - MMA Instituto Bra. **Revista Brasileira de Cartografi a (2017), Edição de Fotogrametia e Sensoriamento Remoto**, v. 69, n. 6, p. 1041–1051, 2017.

SECRETARIAT. **Global Assessment Report on Biodiversity and Ecosystem Services**. Disponível em: <https://ipbes.net/global-assessment>. Acesso em: 17 jun. 2022.

SEPPELT, R.; LAUTENBACH, S.; VOLK, M. Identifying trade-offs between ecosystem services, land use, and biodiversity: A plea for combining scenario analysis and optimization on different spatial scales. **Current Opinion in Environmental Sustainability**, v. 5, n. 5, p. 458–463, 2013.

SLADE, N. A.; RUSSELL, L. A. Distances as Indices to Movements and Home-Range Size From Trapping Records of Small Mammals. **Journal of Mammalogy**, v. 79, n. 1, p. 346– 351, 1998.

SOARES-FILHO, B. et al. Cracking Brazil ’ s Forest Code. **Science**, v. 344, n. April, p. 363– 364, 2014.

SOUZA, C. M. et al. Reconstructing Three Decades of Land Use and Land Cover Changes in Brazilian Biomes with Landsat Archive and Earth Engine. **Remote Sensing**, v. 12, n. 17, p. 2735, 2020.

SOZIO, G.; MORTELLITI, A. Empirical evaluation of the strength of interspecific competition in shaping small mammal communities in fragmented landscapes. **Landscape Ecology**, v. 31, n. 4, p. 775–789, 2016.

SPERA, S. et al. Solos areno-quarzosos no Cerrado: problemas, características e limitação ao uso. **Embrapa Cerrados**, v. 7, p. 1–48, 1999.

STAN, K. et al. Simulating deforestation in Minas Gerais, Brazil, under changing government policies and socioeconomic conditions. **PLoS ONE**, v. 10, n. 9, p. 1–20, 2015.

STRASSBURG, B. B. N. et al. Moment of truth for the Cerrado hotspot. **Nature Ecology and Evolution**, v. 1, n. 4, 2017.

SUÁREZ-CASTRO, A. F. et al. The Scale-Dependent Role of Biological Traits in Landscape Ecology: A Review. **Current Landscape Ecology Reports**, v. 3, n. 1, p. 12–22, 2018.

TAYLOR, P.; BERGALLO, H. D. G. Studies on Neotropical Fauna and Environment Ecology of a small mammal community in an Atlantic forest area in southeastern Brazil Ecology of a Small Mammal Community in an Atlantic Forest Area in Southeastern Brazil. **Studies on Neotropical Fauna and Environment**, v. 4, p. 37–41, 1994.

TURNER, M. G. Landscape Ecology: The Effect of Pattern on Process. **Annual Review of Ecology and Systematics**, v. 20, n. 1, p. 171–197, 1989.

UMETSU, F.; PAUL METZGER, J.; PARDINI, R. Importance of estimating matrix quality for modeling species distribution in complex tropical landscapes: a test with Atlantic forest small mammals. **Ecography**, p. 080304020349105, 4 mar. 2008.

VERBURG, P. H. et al. Land system change and food security: Towards multi-scale land system solutions. **Current Opinion in Environmental Sustainability**, v. 5, n. 5, p. 494– 502, 2013.

VIEIRA, E. M.; BRIANI, D. C. Short-term effects of fire on small rodents in the Brazilian Cerrado and their relation with feeding habits. **International Journal of Wildland Fire**, v. 22, n. 8, p. 1063–1071, 2013.

VIEIRA, M. V. et al. Land use vs. fragment size and isolation as determinants of small mammal composition and richness in Atlantic Forest remnants. **Biological Conservation**, v. 142, n. 6, p. 1191–1200, 2009.

VIEIRA, M. V. et al. Fair tests of the habitat amount hypothesis require appropriate metrics of patch isolation: An example with small mammals in the Brazilian Atlantic Forest. **Biological Conservation**, v. 226, p. 264–270, 2018.

WEAVER, W. Science and Complexity. Em: KLIR, G. J. (Ed.). . **Facets of Systems Science**. International Federation for Systems Research International Series on Systems Science and Engineering. Boston, MA: Springer US, 1991. p. 449–456.

WILENSKY, U.; RAND, W. **An Introduction to Agent-Based Modeling: Modeling Natural, Social, and Engineered Complex Systems with NetLogo**. [s.l.] The MIT Press, 2015.

ZIMBRES, B. et al. The impact of habitat fragmentation on the ecology of xenarthrans (Mammalia) in the Brazilian Cerrado. **Landscape Ecology**, v. 28,

n. 2, p. 259–269, 2013a.

ZIMBRES, B. et al. The impact of habitat fragmentation on the ecology of xenarthrans (Mammalia) in the Brazilian Cerrado. **Landscape Ecology**, v. 28, n. 2, p. 259–269, 2013b.

ZOLLNER, A. Comparing thelandscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes *. 2000.

ZOLLNER, P. A.; LIMA, S. L. Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. **Oikos**, v. 80, n. 1, p. 51–60, 1997.

ZOLLNER, P. A.; LIMA, S. L. Behavioral tradeoffs when dispersing across a patchy landscape. **Oikos**, v. 2, 2005.

APPENDIX A – CHAPTER 4

Table A.1 Area (km2) of Cerrado natural habitats within mechanisms of protection and without any protection.

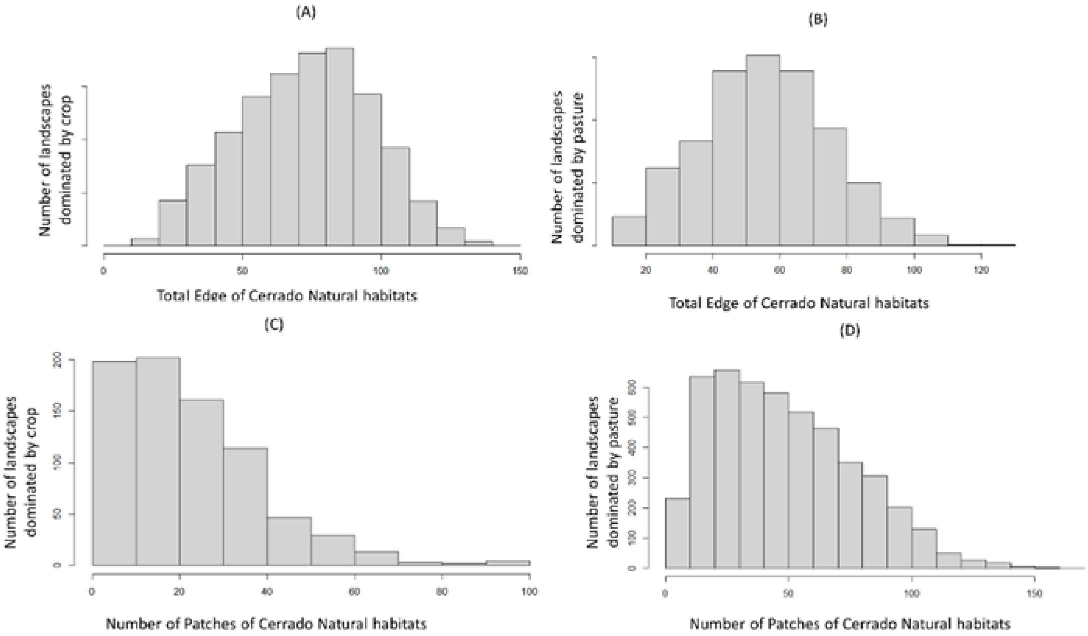
	APP	RL	PA	Without protection	Total Native
Forest	520,256,563.5	1,186,292,240.7	368,619,111.5	1,853,484,251.1	3,928,652,167.7
Savanna	208,492,415.0	1,063,012,206.8	406,452,644.9	2,717,435,760.8	4,395,393,026.4
Grassland	158,626,831.8	637,969,003.8	470,345,418.3	1,762,169,822.4	3,029,111,076.3

Table A.2 Mean values for Percentage of Cerrado, Total Edge, and Number of Patches within the landscapes with the predominance of crops and landscapes with the predominance of pasture.

	Percentage of Cerrado	Total Edge (km)*	Number of Patches*
Crop	10.07214484	55.4893303	22.86028461
Pasture	35.52629153	72.52295086	48.80578684

* values calculated for landscapes with the amount of Cerrado native habitats between 20% and 30%.

Figure A.1 Distribution of the metrics of the Cerrado natural habitats. (A) Total Edge in landscapes dominated by crop; (B) Total Edge in landscape dominated by pasture; (C) Number of Patches in landscapes dominated by crops; and (D) Number of Patches in landscapes dominated by pasture.



Source: The author.

APPENDIX B – CHAPTER 6

Table B.1 Species classified according to the type of Cerrado land cover they use as habitats.

Gender	Species	Cerrado	Ref.
Akodon	*Akodon cursor*	Savanna/Grassland	Patton et al., 2015
	Akodon lindberghi	Forest or gallery forest	Patton et al., 2015
	Akodon montensis	Forest or gallery forest	Patton et al., 2015
Calomys	*Calomys callidus*	Forest or gallery forest	Patton et al., 2015
	Calomys callosus	Savanna/Grassland	Alho et al., 1986
	Calomys expulsus	Savanna/Grassland	Bonvincino et al., 2008
	Calomys tener	Savanna/Grassland	Patton et al., 2015
	Calomys tocantinsi	Savanna/Grassland	Patton et al., 2015
Caluromys	*Caluromys lanatus*	Forest or gallery forest	Mendes-Oliveira et al., 2015
	Caluromys philander	Forest or gallery forest	Mendes-Oliveira et al., 2015
Cerradomys	*Cerradomys maracajuensis*	Savanna/Grassland	Patton et al., 2015
	Cerradomys marinhus	Savanna/Grassland	Patton et al., 2015
	Cerradomys scotti	Savanna/Grassland	Patton et al., 2015
	Cerradomys subflavus	Savanna/Grassland	Patton et al., 2015
Chironectes	*Chironectes minimus*	Forest or gallery forest	Mendes-Oliveira et al., 2015
Clyomys	*Clyomys laticeps*	Savanna/Grassland	Patton et al., 2015
Criptonanus	*Cryptonanus agricolae*	Savanna/Grassland	Alfred e Gardner, 2008
Didelphis	*Didelphis albiventris*	Savanna/Grassland	Alfred e Gardner, 2008
	Didelphis marsupialis	Forest or gallery forest	Alfred e Gardner, 2008
Gracilinanus	*Gracilinanus agilis*	Forest or gallery forest	Alfred e Gardner, 2008
	Gracilinanus emiliae	Forest or gallery forest	Alfred e Gardner, 2008
Micoureus	*Micoureus constantiae*	Forest or gallery forest	Alfred e Gardner, 2008
	Micoureus demerarae	Forest or gallery forest	Alfred e Gardner, 2008
Marmosa	*Marmosa murina*	Forest or gallery forest	Alfred e Gardner, 2008
Marmosops	*Marmosops incanus*	Savanna/Grassland	Alfred e Gardner, 2008
Monodelphis	*Monodelphis americana*	Forest or gallery forest	Alfred e Gardner, 2008
	Monodelphis domestica	Savanna/Grassland	Alfred e Gardner, 2008
	Monodelphis kunsi	Forest or gallery forest	Alfred e Gardner, 2008
Necromys	*Necromys lasiurus*	Savanna/Grassland	Patton et al., 2015
Nectomys	*Nectomys rattus*	Forest or gallery forest	Patton et al., 2015
	Nectomys squamipes	Forest or gallery forest	Patton et al., 2015

Continue

Table B.1 Conclusion.

Gender	Species	Cerrado	Ref.
Oecomys	*Oecomys bicolor*	Forest or gallery forest	Patton et al., 2015
	Oecomys cleberi	Forest or gallery forest	Patton et al., 2015
	Oecomys concolor	Forest or gallery forest	Patton et al., 2015
	Oecomys mamorae	Forest or gallery forest	Patton et al., 2015
	Oecomys roberti	Forest or gallery forest	Patton et al., 2015
Oligoryzomys	*Oligoryzomys chacoensis*	Savanna/Grassland	Patton et al., 2015
	Oligoryzomys fornesi	Forest or gallery forest	Patton et al., 2015
	Oligoryzomys nigripes	Forest or gallery forest	Patton et al., 2015
Oxymycterus	*Oxymycterus delator*	Forest or gallery forest	Patton et al., 2015
Philander	*Philander opossum*	Forest or gallery forest	Alfred e Gardner, 2008
Proechimys	*Proechimys longicaudatus*	Forest or gallery forest	Alfred e Gardner, 2008
	Proechimys roberti	Forest or gallery forest	Alfred e Gardner, 2008
Rhipidomys	*Rhipidomys macrurus*	Savanna/Grassland	Patton et al., 2015
	Rhipidomys mastacalis	Forest or gallery forest	Patton et al., 2015
Thalpomys	*Thalpomys cerradensis*	Forest or gallery forest	Patton et al., 2015
	Thalpomys lasiotis	Forest or gallery forest	Patton et al., 2015
Thrichomys	*Thrichomys apereoides*	Savanna/Grassland	Patton et al., 2015
	Thrichomys pachyurus	Forest or gallery forest	Patton et al., 2015
Thylamys	*Thylamys macrurus*	Forest or gallery forest	Patton et al., 2015
Trinomys	*Trinomys albispinus*	Savanna/Grassland	Patton et al., 2015
Wiedomys	*Wiedomys pyrrhorhinos*	Savanna/Grassland	Patton et al., 2015

APPENDIX C – CHAPTER 7

C.1. Code from the computional model SMAC

```
Part 1 – time & space
-- object that represents time
now = {
   year = , -- initial year
   month = , -- initial month
   day = , -- initial day
   -- current time in the format YYYYMMDD
   get = function(self)
      local mymonth = tostring(self.month)
      if string.len(mymonth) == 1 then mymonth = "0"..mymonth end

      local myday = tostring(self.day)
      if string.len(myday) == 1 then myday = "0"..myday end

      return(tonumber(self.year..mymonth..myday))
   end,

    -- one more day
   -- it assumes each month has 30 days. more accurate solution can be implemented

   nextday = function(self)
      self.day = self.day + 1

      if self.day > 30 then
         self.day = 1
         self.month = self.month + 1

         if self.month > 12 then
            self.month = 1
            self.year = self.year + 1
         end
      end
   end
}
```

```
-- compute the days in the format YYYYDDMM when burning occurs
burningTimes = function()
   local result = {}
   forEachFile("Shapefile/Queimadas",  function(file)
      result[tonumber(file:name():sub(9, 16))] = true
   end)

   return result
end

burningTimes_ = burningTimes()

-- compute the days in the format YYYY0101 when land change updates occur
landChangeTimes = function()
   local result = {}
   forEachFile("Shapefile/Cells", function(file)
      --print("Teste:"..file:name():sub(7,10))
      if string.endswith(file:name(), "shp") then
         result[tonumber(file:name():sub(10, 13).."0101")] = true
      end
   end)

   return result
end

landChangeTimes_ = landChangeTimes()
burning_ = {}

-- each cell has a funcion named burning that returns if it is burning
-- if cell:burning() then ... end
cell = Cell{
   burning = function(self)
      if not burning_[self.x] then return 0 end
      if burning_[self.x][self.y] then return 1 end
      return 0
   end
}


cs = CellularSpace{
   file = "Shapefile/Cells/Grassland2000.shp",
```

```
   instance = cell
}


cs:createNeighborhood{}

updateBurning = function(time)
   burning_ = {}

   if not burningTimes_[time] then return false end

   print("updateBurning "..time)
   local file = "Shapefile/Queimadas/Queimada"..time..".shp.csv"
   local data = File(file):read()

   for i = 1, #data do
      local col = data.col[i]
      if not burning_[col] then
         burning_[col] = {}
      end

      local row = data.row[i]
      burning_[col][row] = true
   end
   return true
end

updateLandCover = function(time)
   if not landChangeTimes_[time] then
      return false
   end

   print("updateLandCover  "..time)

   local file = "Shapefile/Cells/Grassland2000.shp"..string.sub(time, 1, 4)..".shp"
   local cs2 = CellularSpace{file = file}

   forEachCellPair(cs, cs2, function(c1, c2)
      c1.state = c2.state
   end)
```

```
   return true
end
```

Part 2 – Habitat Cone

```
-- compute a set of habitats from the cone using neighbor cells and a radius
habitatCone = function(cell, radius)
   local result = {}
   radius = radius - 1
   local x = cell.x
   local y = cell.y

   local zero_table = function() return {} end
   local whatToDo = function(habitat, mcell)
      table.insert(habitat, mcell)
   end

   --local cs = cell.parent
  local mcell
   local y_1 = cs:get(x, y - 1)
   local habitat

   if y_1 then
      habitat = zero_table()

      for dx = 0, radius do
         local my = y - dx - 1
         for mdx = -dx, dx do
            mcell = cs:get(x + mdx, my)

            if mcell then whatToDo(habitat, mcell) end
         end
      end

      table.insert(result, habitat)
   end

   --------------------------------------------
   y_1 = cs:get(x, y + 1)

   if y_1 then
      habitat = zero_table()
```

```
   for dx = 0, radius do
      local my = y + dx + 1
      for mdx = -dx, dx do
         mcell = cs:get(x + mdx, my)

         if mcell then whatToDo(habitat, mcell) end
      end
   end

   table.insert(result, habitat)
end
---------------------------------------------
local x_1 = cs:get(x - 1, y)

if x_1 then
   habitat = zero_table()
   for dy = 0, radius do
      local mx = x - dy - 1
      for mdy = -dy, dy do
         mcell = cs:get(mx, y + mdy)
         if mcell then whatToDo(habitat, mcell) end
      end
   end

   table.insert(result, habitat)
end

x_1 = cs:get(x + 1, y)

if x_1 then
   habitat = zero_table()

   for dy = 0, radius do
      local mx = x + dy + 1
      for mdy = -dy, dy do
         mcell = cs:get(mx, y + mdy)

         if mcell then whatToDo(habitat, mcell) end
      end
   end
```

```
      table.insert(result, habitat)
   end
--====================================================================

-- DIAGONAL
   y_1 = cs:get(x - 1, y - 1)

   if y_1 then
      habitat = zero_table()

      if y_1 then whatToDo(habitat, y_1) end
      if radius == 1 then
         mcell = cs:get(x - 2, y - 2)
         if mcell then whatToDo(habitat, mcell) end

         mcell = cs:get(x - 2, y - 1)
         if mcell then whatToDo(habitat, mcell) end

         mcell = cs:get(x - 1, y - 2)
         if mcell then whatToDo(habitat, mcell) end
      end

      table.insert(result, habitat)
   end


   y_1 = cs:get(x + 1, y + 1)

   if y_1 then
      habitat = zero_table()

      if y_1 then whatToDo(habitat, y_1) end
      if radius == 1 then
         mcell = cs:get(x + 2, y + 2)
         if mcell then whatToDo(habitat, mcell) end

         mcell = cs:get(x + 2, y + 1)
         if mcell then whatToDo(habitat, mcell) end

         mcell = cs:get(x + 1, y + 2)
         if mcell then whatToDo(habitat, mcell) end
      end
```

```
   table.insert(result, habitat)
end

y_1 = cs:get(x + 1, y - 1)

if y_1 then
   habitat = zero_table()

   if y_1 then whatToDo(habitat, y_1) end
   if radius == 1 then
      mcell = cs:get(x + 2, y - 2)
      if mcell then whatToDo(habitat, mcell) end

      mcell = cs:get(x + 2, y - 1)
      if mcell then whatToDo(habitat, mcell) end

      mcell = cs:get(x + 1, y - 2)
      if mcell then whatToDo(habitat, mcell) end
   end

   table.insert(result, habitat)
end

y_1 = cs:get(x - 1, y + 1)

if y_1 then
   habitat = zero_table()
   if y_1 then whatToDo(habitat, y_1) end
   if radius == 1 then
      mcell = cs:get(x - 2, y + 2)
      if mcell then whatToDo(habitat, mcell) end

      mcell = cs:get(x - 2, y + 1)
      if mcell then whatToDo(habitat, mcell) end

      mcell = cs:get(x - 1, y + 2)
      if mcell then whatToDo(habitat, mcell) end
   end

   table.insert(result, habitat)
```

```
    end

    return result
end


cs = CellularSpace{xdim = 10}

cell = cs:sample()
print(cell.x.." "..cell.y)
print("========================")
cone = habitatCone(cell, 2)

forEachElement(cone, function(idx, set)
    print(idx)
    forEachElement(set, function(_, mcell)
        print(mcell.x.." "..mcell.y)
    end)
end)
```

Part 3 - Main

```
dofile("timeAndSpace.lua")
dofile("habitatCone.lua")
dofile("queue.lua")

-- a habitat is a vector of cells
habitatDensity = function(habitat, self)
    local sum = 0

    if self then sum = -1 end
    forEachElement(habitat, function(_, cell)
        sum = sum + #cell:getAgents()
    end)

    return sum / #habitat
end

habitatBurning = function(habitat)
    local burning = false
```

```
    forEachElement(habitat, function(_, cell)
        if cell:burning() == 1 then
            burning = true
        end
    end)

    return burning
end


Mouse = Agent{
    -- verifica se o habitat esta cheio
    fullHabitat = function(self, habitat)
        if habitat == nil then
            return habitatDensity(self.habitat, true) > self.density
        end

        return habitatDensity(habitat) > self.density
    end,
    -- move the agent to a random cell within its habitat
    moveWithinHabitat = function(self)
        local newCell = Random(clone(self.habitat)):sample()

        if newCell:isEmpty() then
            self:move(newCell)
        end
    end,
    validHabitat = function(self, cell)
        return belong(cell.state, self.validHabitats)
    end,
    validHidro = function(self, cell)
        return cell.Hidro_dist < self.hidroDist
    end,
    validSwim = function(self, cell)
        return cell.Hidro_dist == 0 and self.swim == false
```

```
end,

habitatGrade = function(self, habitat)
   local grade = 0

   forEachElement(habitat, function(_,
      cell) if self:validHidro(cell) then
        grade = grade +
      1 end
      if self:validSwim(cell)
         then grade = grade - 1
      end
      if self:validHabitat(cell)
         then if self[cell.state] ==
         nil then
            print(cell.state)
            print(self)
         end
         grade = grade +
      self[cell.state] end

   end)

   return grade
end,
newHabitat =
   function(self)
   self.habitat = {}
end,
addHabitat = function(self,
   cell) if type(cell) ~= "Cell"
   then
      error("wrong cell, got "..type(cell))
   end

   table.insert(self.habitat,
cell) end,
checkCone = function(self)
   local candidates = habitatCone(self:getCell(), 2)

   local best_candidates = {}
   local best_grade = self:habitatGrade(self.habitat)
   local newCell

   if self:fullHabitat() then
```

```
        best_grade = 0
    end
    forEachElement(candidates, function(_,
        habitat) if habitatBurning(habitat) then
        return end
        if self:fullHabitat(habitat) then return end

        local grade = self:habitatGrade(habitat)

        if grade > best_grade then
            best_candidates = {habitat}
            best_grade = grade

        elseif grade == best_grade then
            table.insert(best_candidates, habitat)
        e
    nd
    en
    d)

    if #best_candidates > 1 then
        newCell =
    Random(best_candidates):sample()[1] elseif
    #best_candidates == 1 then
        newCell =
    best_candidates[1][1] end

    if newCell then -- compute the new habitat
       -- print("new cell")

        self:move(newCell)
        self:buildHabitat(newCell)
    e
nd
en
d,
buildHabitat = function(self, cell)
--
      print("buildHabita
    t") self:move(cell)
    local addedToQueue =
    {} self:newHabitat()

    queue:clean()
    queue:push(cell)
```

```
addedToQueue[cell] =
true

local missing = self.lifearea
local i = 0
while missing > 0 and queue:length() > 0 do
   local candidates = {}
   i = i + 1
   for _ = 1, queue:length() do
      local newcell =
      queue:pop()
      newcell.mcandidate = i

      if self:validHabitat(newcell)
         then table.insert(candidates,
         newcell)

         forEachNeighbor(newcell,
            function(neigh) if not
            addedToQueue[neigh] then
               addedToQueue[neigh] =
               true queue:push(neigh)
            e
         nd
         en
         d)
      e
   nd
   en
   d

--    print("candidates:
   "..#candidates) if #candidates <=
   missing then
  --      print("add all")
      forEachElement(candidates, function(_, value)
         self:addHabitat(value)
      end)

      missing = missing - #candidates
   else -- #candidates > missing
--       print("add
      "..missing) while
      missing > 0 do
         local pos = Random{min = 1, max = #candidates, step = 1}:sample()
```

```
               self:addHabitat(candidates[pos]
               ) table.remove(candidates,
               pos) missing = missing - 1
            e
         nd
         en
         d
      --    print("allocated:
      "..#self.habitat) end
      --print(#self.habitat)

      if #self.habitat == 0 then -- could not find any cell
         self:addHabitat(self:getCell())
      e
   nd
   en
   d,
   execute = function(self)
      self:checkCone()
      self:moveWithinHabitat
      () self:lifeCycle()
   end,
   procreate = function(self)
      local new_mouse = self:reproduce()
      new_mouse:newHabitat()
      new_mouse:addHabitat(new_mouse:getCell(
      ))
   end,
   lifeCycle = function(self)
      self.Age = self.Age + 1
      --print(self.Age.."  "..self.ReproductiveAge.. "  "..tostring(self:fullHabitat()).. "
"..self.sex)

      forEachElement(self.habitat, function(_, habitat_unit)
         --forEachElement(self.validHabitats, function(_, validHabitats_unit)
               --if habitat_unit.state == validHabitats_unit then
               if belong(habitat_unit.state, self.validHabitats) then
                  -- reproductiveAge = 10, betweenoffspring = 4 => 10, 14, 18, 22,
                  etc. if self.sex == "female" and (self.Age >= self.ReproductiveAge)
                  and not
self:fullHabitat() then

                  --if self.sex == "female" and not self:fullHabitat() and (self.Age >=
self.ReproductiveAge) then
```

```
              -- se o habitat estiver cheio na epoca da reproducao ela vai perder a
janela de reproducao
              --print((self.Age - self.ReproductiveAge) % self.BetweenOffspring)
              if (self.Age - self.ReproductiveAge) % self.BetweenOffspring == 0 then
              -
- a cada ReproductiveAge dias
                --print("reproduce
                "..self.Offspring) for _ = 1,
                self.Offspring do
                  self:procreat
                e() end

                local prob = self.Offspring % 1 -- 4.2 => 4 mouses + 20% of change of
one more mouse

                if Random{p = prob}:sample() then
                  self:procreate()
                e
              nd
              en
              d
            e
          nd
          en
          d
      end)
    --end)

    if self.Age > self.LifeExpectance then
      --print("die")
      self:die()
   elseif self:getCell():burning() == 1 and Random{p =
 self.BurningProbability}:sample() then
      self:die(
    ) end
  end
}


animal1 = Mouse{
  Offspring = ,
  ReproductiveAge = ,
  BurningProbability =
  , BetweenOffspring
  = ,
  LifeExpectance = Random{mean = , sd =
```

```
   }, sex = Random {"male", "female"},
   Age = ,
   forest = ,
   savanna
   = ,
   grassland
   = , crop =,
   pasture =
   ,
   OtherNonVegetatedArea
   = , ForestPlantation = ,
   Water = ,
   MosaicAgriculturePasture
   = , Wetland  = ,
   Rockyoutcrop
   = , Others = ,
   density = ,
   lifearea = ,
   perceptualRange
   = , validHabitats =
   {""}, hidroDist = ,
   swim = false
}

soc1 = Society{instance = animal1, quantity = 100}

env = Environment{soc1, cs}
env:createPlacement{}

-- the initial habitat of an agent is the cell it belongs
-- from the first step on it will be the cone it moved to
forEachCell(cs, function(cell)
   local agent = cell:getAgent()
   if agent then
      agent:newHabitat()
      agent:addHabitat(cell)
   e
nd
en
d)

currentTime = now:get()

map = Map{
   target = cs,
```

```
   select =
   "state",
    value = {"forest", "savanna", "grasslands", "pasture", "crop"},
   --value = {3, 4, 12, 15}, --"4", "12", "15", "19", "21", "33"},
   color = {"green","yellow", "orange", "red", "purple"}
}

map2 =
   Map{
   target =
   cs,
   select = "burning",
    value = {0,1},
   color = {"white","red"}
}


map2 = Map{
   target =
   soc4,
   background = map2
}

quantityByClass = File("1-quantity-by-class.csv")
quantityByCoverage = File("1-quantity-by-
coverage.csv")
quantityByClassAndCoverage = File("1-quantity-by-class-and-coverage.csv")

land_classes = {"forest", "savanna", "grassland", "crop", "pasture",
"OtherNonVegetatedArea",
   "ForestPlantation", "water", "MosaicAgriculturePasture", "Wetland",
"Rockyoutcrop",
   "urban", "minning"}
agent_classes = {"s1", "s2", "s3", "s4"}

quantityByClass:writeLine({"time","s1", "s2", "s3", "s4", "total"}, ";")

quantityByCoverage:writeLine({"time","forest", "grassland", "pasture", "savanna",
"crop", "total"}, ";")

header = {"time"}

forEachElement(agent_classes, function(_, agent_class)
   forEachElement(land_classes, function(_, land_class)
      table.insert(header,
   agent_class.."_"..land_class) end)
```

```
end)

quantityByClassAndCoverage:writeLine(header,

";") writeByClass = function()
  quantityByClass:writeLine({currentTime, #soc1, #soc2, #soc3, #soc4, #soc1 + #soc2 +
#soc3 + #soc4}, ";")
end

writeByClassAndCoverage = function()
   local societies = {s1 = soc1, s2 = soc2, s3 = soc3, s4 =

   soc4} local sum = {}

   forEachElement(agent_classes, function(_, agent_class)
      sum[agent_class] = {}
      forEachElement(land_classes, function(_, land_class)
         sum[agent_class][land_class] = 0
      en
   d)
   end)

   forEachElement(societies, function(name, soc)
      forEachAgent(soc, function(ag)
         local state = ag:getCell().state
         --if state == "grassland" then state = "grasslands"
         end if sum[name][state] == nil then
            print(">>> "..ag:getCell().state)
         end
         sum[name][state] = sum[name][state] + 1
      end)
   end)

   local line = {currentTime}

   forEachElement(agent_classes, function(_,

   agent_class)
      forEachElement(land_classes,  function(_,  land_class)
         table.insert(line,
      sum[agent_class][land_class]) end)
   end)

   quantityByClassAndCoverage:writeLine(line,
";") end
```

```
writeByCoverage = function()
   local sum = {forest = 0, grassland = 0, pasture = 0, savanna = 0, crop = 0}

   forEachCell(cs, function(cell)
      if sum[cell.state] == nil then return
      end if cell:getAgent() == nil then
      return end

      sum[cell.state] = sum[cell.state] + 1
   end)

   quantityByCoverage:writeLine({currentTime, sum.forest, sum.grassland,
sum.pasture, sum.savanna, sum.crop,
                          sum.forest + sum.grassland + sum.pasture + sum.savanna +
sum.crop},
";") end

writeByCoverage()
writeByClass()
writeByClassAndCoverage()

updateHabitat = function()
   forEachCell(cs,
   function(cell)
      cell.totHabitat = 0
   end)

   forEachCell(cs, function(cell)
      local agent =
      cell:getAgent()

      if agent then
         forEachElement(agent.habitat, function(_,
            mcell) mcell.totHabitat = mcell.totHabitat + 1

            if mcell.totHabitat > 4 then mcell.totHabitat = 4 end
         end)

         --cell.totHabitat =
      5 end
   end)
end

updateHabitat
```

```
()


m4 = Map{
   target =
   cs,
   select = "totHabitat",
   value = {0, 1, 2, 3, 4, 5},
   color = {"white", "lightBlue", "blue", "blue", "darkBlue", "red"}
}

]]--

cleanCandidate = function()
   forEachCell(cs,
   function(cell)
      cell.mcandidate = 0
   end)
end

cleanCandidat

e

m5 = Map{
   target =
   cs,
   select = "mcandidate",
   value = {0, 1, 2, 3, 4,
   5},
   color = {"white", "lightBlue", "blue", "darkBlue", "yellow", "red"}
}

cell_size = Cell{
   soc1 = function() return #soc1
   end, soc2 = function() return
   #soc2 end, soc3 = function()
   return #soc3 end, soc4 =
   function() return #soc4 end,
}

chart_size =
   Chart{ target =
   cell_size,
   select = {"soc1", "soc2", "soc3", "soc4"},
   color = {"red", "green", "blue", "magenta"}
```

```
}

step = 1
while currentTime < 20180101 do -- final time
   cleanCandidate()
   print(currentTime.." "..os.date())
   updateHabitat()
   currentTime = now:get()
   --[[if updateLandCover(currentTime)
      then map:update()
   end
   if updateBurning(currentTime) then
      map2:update()
   end]]--
   --m4:update()
   soc1:execute()
   soc2:execute()
   soc3:execute()
   soc4:execute()
   now:nextday()
   writeByClass()
   writeByCoverage()
   writeByClassAndCoverag
   e()
   --m5:update()
   --
   chart_size:update(step
   ) step = step + 1
   collectgarbage("collect
   ")
End
```

C.2. Tables

Table C.1 Literature review of general information for 53 species.

Species	**Geographic distribution**	**Reference**	**Habit**	**Reference**	**Diet**	**Reference**	**Size**	**Reference**
Akodon cursor	widly	Paglia et al., 2012	cursorial	Paglia et al., 2012	insectivorous	Paglia et al., 2012	50-150g	Paglia et al., 2012
Akodon lindberghi	widly	Paglia et al., 2012	cursorial	Paglia et al., 2012	insectivorous	Paglia et al., 2012	0-50g	Paglia et al., 2012
Akodon montensis	mean	Paglia et al., 2012	cursorial	Paglia et al., 2012	insectivorous	Paglia et al., 2012	0-50g	Paglia et al., 2012
Calomys callidus	mean	Paglia et al., 2012	cursorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	0-50g	Paglia et al., 2012
Calomys callosus	mean	Paglia et al., 2012	cursorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	0-50g	Paglia et al., 2012
Calomys expulsus	widly	Paglia et al., 2012	cursorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	0-50g	Paglia et al., 2012
Calomys tener	mean	Paglia et al., 2012	cursorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	0-50g	Paglia et al., 2012
Calomys tocantinsi	widly	Paglia et al., 2012	cursorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	0-50g	Paglia et al., 2012
Caluromys lanatus	mean	Paglia et al., 2012	arboreal	Paglia et al., 2012	frugivore	Paglia et al., 2012	150-500g	Paglia et al., 2012
Caluromys philander	mean	Paglia et al., 2012	arboreal	Paglia et al., 2012	frugivore	Paglia et al., 2012	150-500g	Paglia et al., 2012
Cerradomys maracajuensis	widly	Paglia et al., 2012	cursorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	50-150g	Paglia et al., 2012
Cerradomys marinhus	widly	Paglia et al., 2012	cursorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	50-150g	Paglia et al., 2012
Cerradomys scotti	mean	Paglia et al., 2012	cursorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	50-150g	Paglia et al., 2012
Cerradomys subflavus	mean	Paglia et al., 2012	cursorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	50-150g	Paglia et al., 2012
Chironectes minimus	mean	Paglia et al., 2012	semi aquatic	Paglia et al., 2012	piscivorous	Paglia et al., 2012	500-1,000g	Paglia et al., 2012
Clyomys laticeps	mean	Paglia et al., 2012	fossorial	Paglia et al., 2012	herbivore	Paglia et al., 2012	150-500g	Paglia et al., 2012
Cryptonanus agricolae	widly	Paglia et al., 2012	arboreal	Paglia et al., 2012	omnivorous	Paglia et al., 2012	0-50g	Paglia et al., 2012
Didelphis albiventris	mean	Paglia et al., 2012	scansorial	Paglia et al., 2012	omnivorous	Paglia et al., 2012	1-2kg	Paglia et al., 2012
Didelphis marsupialis	mean	Paglia et al., 2012	scansorial	Paglia et al., 2012	omnivorous	Paglia et al., 2012	1-2kg	Paglia et al., 2012
Gracilinanus agilis	mean	Paglia et al., 2012	arboreal	Paglia et al., 2012	omnivorous	Paglia et al., 2012	0-50g	Paglia et al., 2012
Gracilinanus emiliae	mean	Paglia et al., 2012	arboreal	Paglia et al., 2012	omnivorous	Paglia et al., 2012	0-50g	Paglia et al., 2012

Continue

Table C.1 Continuation.

Species	Geographic distribution	Reference	Habit	Reference	Diet	Reference	Size	Reference
Micoureus constantiae	mean	Paglia et al., 2012	arboreal	Paglia et al., 2012	omnivorous	Paglia et al., 2012	50-150g	Paglia et al., 2012
Micoureus demerarae	mean	Paglia et al., 2012	arboreal	Paglia et al., 2012	omnivorous	Paglia et al., 2012	50-150g	Paglia et al., 2012
Marmosa murina	mean	Paglia et al., 2012	scansorial	Paglia et al., 2012	insectivorous	Paglia et al., 2012	50-150g	Paglia et al., 2012
Marmosops incanus	widly	Paglia et al., 2012	scansorial	Paglia et al., 2012	insectivorous	Paglia et al., 2012	0-50g	Paglia et al., 2012
Monodelphis americana	mean	Paglia et al., 2012	cursorial	Paglia et al., 2012	insectivorous	Paglia et al., 2012	0-50g	Paglia et al., 2012
Monodelphis domestica	mean	Paglia et al., 2012	cursorial	Paglia et al., 2012	insectivorous	Paglia et al., 2012	50-150g	Paglia et al., 2012
Monodelphis kunsi	mean	Paglia et al., 2012	cursorial	Paglia et al., 2012	insectivorous	Paglia et al., 2012	0-50g	Paglia et al., 2012
Necromys lasiurus	mean	Paglia et al., 2012	cursorial	Paglia et al., 2013	frugivore	Paglia et al., 2012	50-150g	Paglia et al., 2012
Nectomys rattus	mean	Paglia et al., 2012	semi aquatic	Paglia et al., 2012	frugivore	Paglia et al., 2012	150-500g	Paglia et al., 2012
Nectomys squamipes	mean	Paglia et al., 2012	semi aquatic	Paglia et al., 2012	frugivore	Paglia et al., 2012	150-500g	Paglia et al., 2012
Oecomys bicolor	mean	Paglia et al., 2012	arboreal	Paglia et al., 2012	frugivore	Paglia et al., 2012	0-50g	Paglia et al., 2012
Oecomys cleberi	restricted	Paglia et al., 2012	arboreal	Paglia et al., 2013	frugivore	Paglia et al., 2012	0-50g	Paglia et al., 2012
Oecomys concolor	mean	Paglia et al., 2012	arboreal	Paglia et al., 2012	frugivore	Paglia et al., 2012	0-50g	Paglia et al., 2012
Oecomys mamorae	mean	Paglia et al., 2012	arboreal	Paglia et al., 2012	frugivore	Paglia et al., 2012	50-150g	Paglia et al., 2012
Oecomys roberti	mean	Paglia et al., 2012	arboreal	Paglia et al., 2012	frugivore	Paglia et al., 2012	150-500g	Paglia et al., 2012
Oligoryzomys chacoensis	mean	Paglia et al., 2012	scansorial	Paglia et al., 2013	frugivore	Paglia et al., 2012	0-50g	Paglia et al., 2012
Oligoryzomys fornesi	mean	Paglia et al., 2012	scansorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	0-50g	Paglia et al., 2012
Oligoryzomys nigripes	mean	Paglia et al., 2012	scansorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	0-50g	Paglia et al., 2012
Oxymycterus delator	mean	Paglia et al., 2012	fossorial	Paglia et al., 2012	insectivorous	Paglia et al., 2012	50-150g	Paglia et al., 2012
Philander opossum	mean	Paglia et al., 2012	scansorial	Paglia et al., 2013	insectivorous	Paglia et al., 2012	500-1,000g	Paglia et al., 2012
Proechimys longicaudatus	mean	Paglia et al., 2012	cursorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	150-500g	Paglia et al., 2012
Proechimys roberti	widly	Paglia et al., 2012	cursorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	150-500g	Paglia et al., 2012
Rhipidomys macrurus	widly	Paglia et al., 2012	arboreal	Paglia et al., 2012	frugivore	Paglia et al., 2012	50-150g	Paglia et al., 2012

Continue

Table C.1 Conclusion.

Species	**Geographic distribution**	**Reference**	**Habit**	**Reference**	**Diet**	**Reference**	**Size**	**Reference**
Rhipidomys mastacalis	widly	Paglia et al., 2012	arboreal	Paglia et al., 2013	frugivore	Paglia et al., 2012	50-150g	Paglia et al., 2012
Thalpomys cerradensis	widly	Paglia et al., 2012	cursorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	0-50g	Paglia et al., 2012
Thalpomys lasiotis	widly	Paglia et al., 2012	cursorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	0-50g	Paglia et al., 2012
Thrichomys apereoides	mean	Paglia et al., 2012	cursorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	150-500g	Paglia et al., 2012
Thrichomys pachyurus	widly	Paglia et al., 2012	cursorial	Paglia et al., 2013	frugivore	Paglia et al., 2012	150-500g	Paglia et al., 2012
Thylamys macrurus	mean	Paglia et al., 2012	scansorial	Paglia et al., 2012	insectivorous	Paglia et al., 2012	0-50g	Paglia et al., 2012
Trinomys albispinus	widly	Paglia et al., 2012	cursorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	150-500g	Paglia et al., 2012
Wiedomys pyrrhorhinos	widly	Paglia et al., 2012	scansorial	Paglia et al., 2012	frugivore	Paglia et al., 2012	0-50g	Paglia et al., 2012

Table C.2 Literature review of the life cycle for 53 species.

Species	Offspring	Reference	Reproductive age (days)	Time between consecutive offspring (days)	Reference	Life expectance	Ref.
Akodon cursor	4.64	Patton et al, 2015	240	23	Mello and Mathias (1987)		
Akodon lindberghi	2.72	Patton et al, 2015	50	23	De Conto e Cerqueira, 2007	1,359	De Conto and Cerqueira 2007). Experimento em laboratório
Akodon montensis	4	Patton et al, 2015	90	120	Caldara, 2014	660	Putker et al., 2013. Estimado devido escassez de dado na literatura
Calomys callidus							
Calomys callosus	6.25	Patton et al, 2015					
Calomys expulsus	5.87	Araripe et al, 2006					
Calomys tener	3.5	Araripe et al, 2006					
Calomys tocantinsi	7.3	Patton et al, 2015					
Caluromys lanatus	3.5	Alfred					
Caluromys philander	3.5	Alfred		140	Alfred	912	Alfred
Cerradomys maracajuensis	3	Patton et al, 2015					
Cerradomys marinhus	3	Patton et al, 2015					
Cerradomys scotti	4.5	Bonvincino et al., 2012					
Cerradomys subflavus	3	Silva et al., 2015					
Chironectes minimus	3	Alfred				1060	Marshall, 1978
Clyomys laticeps	1	Patton et al, 2015					
Cryptonanus agricolai							

Continue

Table C.2 Continuation.

Species	**Offspring**	**Reference**	**Reproductive age (days)**	**Time between consecutive offspring (days)**	**Reference**	**Life expectance**	**Ref.**
Didelphis albiventris	6.5	Cerqueira, 1984	213	180	Kajin et al., 2008/Rigueiraetal1987	300	Kajin et al, 2008
Didelphis marsupialis	6.54	Tindale e Biscoe, 1976				217	O`Conell, 1989
Gracilinanus agilis	2.66	Puida e Paglia, 2015		Semélparos	Lope e Leiner, 2015	92.6	Mares e Ernest, 1995
Gracilinanus emiliae							
Marmosa murina		Alfred					
Marmosops incanus						142	Passamani e Rosa, 2015
Micoureus constantiae	5	Alfred					
Micoureus demerarae	8	Alfred	180		Brito e Fernandez, 2000	730	Brito e Fernandez, 2000
Monodelphis americana							
Monodelphis domestica	8.4	Alfred	180	20	Macrini, 2004	1170	Macrini, 2004
Monodelphis kunsi							
Necromys lasiurus	4.2	Patton et al, 2015					
Nectomys rattus							
Nectomys squamipes	4.5	Patton et al, 2015		25	Patton et al., 2015	114	Mares e Ernest, 1995
Oecomys bicolor	2	Patton et al, 2015				60	Mares e Ernest, 1995
Oecomys cleberi	2.9	Silva et al., 2015					
Oecomys concolor						60	Mares e Ernest, 1995
Oecomys mamorae	2	Silva et al., 2015					
Oecomys roberti	2.5	Patton et al, 2015					
Oligoryzomys chacoensis	4.6	Patton et al, 2015					

Continue

Table C.2 Conclusion.

Species	**Offspring**	**Reference**	**Reproductive age (days)**	**Time between consecutive offspring (days)**	**Reference**	**Life expectance**	**Ref.**
Oligoryzomys fornesi	2	Silva et al., 2015					
Oligoryzomys nigripes	4.7	Patton et al, 2015					
Oxymycterus delator	4	Patton et al, 2015					
Philander opossum	5.5	Alfred	240	90	Alfred	900	Castro-Arellano et al., 2000
Proechimys longicaudatus							
Proechimys roberti	2.1	Silva et al., 2015					
Rhipidomys macrurus	3.5	Silva et al., 2015				87	Mares e Ernest, 1995
Rhipidomys mastacalis	3	Mares et al., 1989				355	O'Conell, 1989
Thalpomys cerradensis							
Thalpomys lasiotis	2.5	Patton et al, 2015				270	Ribeiro et al., 2011
Thrichomys apereoides	2	Silva et al., 2015		97	Reis e Pêssoa, 2004	110.3	Reis e Pessôa, 2004
Thrichomys pachyurus	2.5	Teixeira 2005		194	Borodin et al., 2006		
Thylamys macrurus							
Trinomys albispinus	3	Patton et al, 2015					
Wiedomys pyrrhorhinos	5.6	Sobral e Oliveira, 2014	83		Sobral e Oliveira, 2014		

Table C.3 Literature review of the use of space for 53 species.

Species	Density (ind/ha)	Ref.	Home range (ha)	Ref.	Perceptual Range	Reference
Akodon cursor	2.72	Cerqueira et al., 1993	0.28 ha	Patton et al, 2015		
Akodon lindberghi	2.72	Queirolo e Granzinolli 2009	0.28 ha	Patton et al, 2016		
Akodon montensis	8.3	Putker et al., 2013	0.61 ha	Fontes et al., 2007	30	Assis 2014
Calomys callidus						
Calomys callosus						
Calomys expulsus	5	Camargo et al., 2018				
Calomys tener	2.5	Camargo et al., 2018				
Calomys tocantinsi						
Caluromys lanatus	0.93	Emmons et al., 1984				
Caluromys philander	0.69	Alfred				
Cerradomys maracajuensis						
Cerradomys marinhus						
Cerradomys scotti	3	Camargo et al., 2018				
Cerradomys subflavus						
Chironectes minimus	1.34	Galliez et al., 2009				
Clyomys laticeps	3.51	Lacher e Alho, 1989				
Cryptonanus agricolai						
Didelphis albiventris	3	Mendel et al., 2008	2.765	Sanches et al., 2012	100 (pasto) 50 (milho) 30 (sujo)	Sanches et al., 2021
Didelphis marsupialis	2	Sunquist et al., 1987				
Gracilinanus agilis	30	Camargo et al., 2018				
Gracilinanus emiliae						
Micoureus constantiae						

Continue

Table C.3 Continuation.

Species	Density (ind/ha)	Ref.	Home range (ha)	Ref.	Perceptual Range	Reference
Micoureus demerarae	1.75	Quental et al., 2001				
Marmosa murina						
Marmosops incanus	13.05	Ferreira et al., 2016				
Monodelphis americana	2	Mares e Ernest, 1985				
Monodelphis domestica	4	Macrini, 2004	0,14991	Macrini 2004		
Monodelphis kunsi	1	Câmara e Oliveira, 2012				
Necromys lasiurus	1 ou 19	Camargo et al., 2018 e Becker et al., 2007				
Nectomys rattus	6	Ernest e Mares, 1995				
Nectomys squamipes	3.4	Patton et al, 2015				
Oecomys bicolor	5	Mares e Ernest, 1995				
Oecomys cleberi						
Oecomys concolor	9	Mares e Ernest, 1995				
Oecomys mamorae						
Oecomys roberti	1	Santos-Filho et al., 2012				
Oligoryzomys chacoensis						
Oligoryzomys fornesi						
Oligoryzomys nigripes	4.62	Putker et al., 2008				
Oxymycterus delator						
Philander opossum	1.91	Cerqueira et al., 1993			100	Forero-Medina e Vieira 2008
Proechimys longicaudatus						
Proechimys roberti						
Rhipidomys macrurus	9	Camargo et al., 2018				

Continue

Table C.3 Conclusion.

Species	Density (ind/ha)	Ref.	Home range (ha)	Ref.	Perceptual Range	Reference
Rhipidomys mastacalis	1.1	O'Conell, 1989				
Thalpomys cerradensis						
Thalpomys lasiotis	1.55	Ribeiro et al., 2011				