UNIVERSIDADE FEDERAL DE VIÇOSA

Ecological implications of direct, indirect and evolutionary effects of fire on neotropical vertebrates

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Magister Scientiae

VIÇOSA - MINAS GERAIS
2025

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Dissertation submitted to the Forest Science Graduate Program of the Universidade Federal de Viçosa in partial fulfillment of the requirements for the degree of *Magister Scientiae*.

Adviser: Fillipe T. Pereira Torres

Co-adviser: Christian Niel Berlinck

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Ficha catalográfica elaborada pela Biblioteca Central da Universidade Federal de Viçosa - Campus Viçosa

T

P436e
2025

Pereira, Alessandra Rezende, 1994-
Ecological implications of direct, indirect and evolutionary effects of fire on neotropical vertebrates / Alessandra Rezende Pereira. – Viçosa, MG, 2025.
1 dissertação eletrônica (101 f.): il. (algumas color.).

Texto em inglês.
Orientador: Fillipe Tamiozzo Pereira Torres.
Dissertação (mestrado) - Universidade Federal de Viçosa, Departamento de Engenharia Florestal, 2025.
Inclui bibliografia.
DOI: https://doi.org/10.47328/ufvbbt.2025.562
Modo de acesso: World Wide Web.

1. Animais - Brasil - Efeito do fogo. 2. Vertebrados. I. Torres, Fillipe Tamiozzo Pereira, 1979-. II. Universidade Federal de Viçosa. Departamento de Engenharia Florestal. Programa de Pós-Graduação em Ciência Florestal. III. Título.

GFDC adapt. CDD 634.9437

Bibliotecário(a) responsável: Euzébio Luiz Pinto CRB-6/3317

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APPROVED: July 28, 2025.

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Aos meus pais, Leila e Reinaldo, que caminharam sob muito sol,
para que eu chegasse até aqui, na sombra.

ACKNOWLEDGMENTS

Durante a construção dessa pesquisa, muitas pessoas foram fundamentais para chegar até aqui. Meus pais, sou grata por acreditarem que a educação transforma vidas e se esforçarem para que eu pudesse fazer essas escolhas durante toda a minha caminhada. Andressa, minha querida irmã, meu exemplo de persistência e dedicação na vida acadêmica, obrigada por me amparar e orientar desde pequenininha. Igor, obrigada por sempre ser amor nos dias difíceis, incentivo nos momentos inseguros, por me ajudar com todas as análises dessa pesquisa e celebrar todos os meus esforços. Thiago, você sempre será fundamental em todas as etapas da minha formação, obrigada pelo seu companheirismo! Kamila, Laura e todas minhas queridas amigas, agradeço por sempre ter em vocês carinho e escuta sincera. Também agradeço a toda minha família, que mesmo distante, sempre torcem por mim.

Aos meus orientadores, Fillipe e Christian, sou grata pela disponibilidade, pela orientação e por fazerem parte do meu crescimento. À equipe do Laboratório de Incêndios e Conservação da Natureza, especialmente ao Gilberto, por ser alegria no dia a dia e por toda sua contribuição nos campos desta pesquisa; e a Monique, por dividir anseios, questionamentos e me receber em Viçosa com carinho. Aos colegas e professores do Programa de Pós-Graduação em Ciência Florestal; e aos companheiros de inglês no Celin. Agradeço também a minha amiga Pilar, pela sua ajuda com a identificação dos animais no Capítulo 1 e 2, ao André e ao Victor (da UFJF) e todos os especialistas em identificação; e a Luiza (também da UFJF) por contribuir sempre com as minhas dúvidas estatísticas.

This work has been sponsored by the following Brazilian research agencies: Coordination for the Improvement of Higher Education Personnel (CAPES; Financing code 001), Minas Gerais State Foundation for Research Aid (FAPEMIG) and National Council of Scientific and Technological Development (CNPq).

“*Estar viva é estar curiosa*.” (Laura Riding)

ABSTRACT

PEREIRA, Alessandra Rezende, M.Sc., Universidade Federal de Viçosa, July, 2025. **Ecological implications of direct, indirect and evolutionary effects of fire on neotropical vertebrates**. Adviser: Fillipe Tamiozzo Pereira Torres. Co-adviser: Christian Niel Berlinck.

The impacts of fire on terrestrial fauna are broad and vary according to species and their ecology. This dissertation is divided into three chapters that aim to understand the relationship between fire and its direct, indirect, and evolutionary effects on vertebrates in Brazil. In Chapters 1 and 2, we assessed the direct and indirect impacts of fire on Brazilian terrestrial vertebrates, based on data obtained through citizen science. The most negatively affected taxonomic groups were identified, as well as those with the highest survival rates and the ecosystem services they provide. The results demonstrate that small-bodied vertebrates (<1 kg), especially reptiles (59.1%), are the most vulnerable. Mammals (28.2%) are also impacted, with implications for crucial ecosystem services such as disease surveillance, seed dispersal, ecotourism, and others. Larger vertebrates (>7 kg) showed the highest survival rates. Species such as Ozotoceros bezoarticus, Rhea americana, birds, Didelphidae, Myrmecophaga tridactyla, and Chelonoidis spp. stood out as those with the greatest likelihood of survival, while also contributing to seed dispersal services. In Chapter 3, we estimated the number of underground openings that wildlife can use as refuges against fire in grassland habitats of Serra da Canastra National Park. These estimates indicate approximately 280.70 openings per hectare, which maintain thermal equilibrium when external temperatures are extremely high due to the heat of the flames. Thus, the findings of this dissertation contribute to our understanding of fire ecology and the interactions between fire and wildlife in Brazilian biomes. Furthermore, they provide important support for biodiversity conservation and fire management, reinforcing that well-planned prescribed burns, which promote environmental heterogeneity and preserve underground refuges, are valuable tools for mitigating negative impacts on wildlife and for sustaining the ecosystem services these species provide.

Keywords: fire impacts; fire ecology; prescribed burns; wildfire; fauna; Brazil

RESUMO

PEREIRA, Alessandra Rezende, M.Sc., Universidade Federal de Viçosa, julho de 2025. **Implicações ecológicas dos efeitos diretos, indiretos e evolutivos do fogo em vertebrados neotropicais**. Orientador: Fillipe Tamiozzo Pereira Torres. Coorientador: Christian Niel Berlinck.

Os impactos do fogo sobre a fauna terrestre são amplos e variam de acordo com as espécies e sua ecologia. Esta dissertação está dividida em três capítulos que, em conjunto, buscam compreender a relação entre o fogo e os seus efeitos diretos, indiretos e evolutivos sobre os vertebrados do Brasil. No Capítulo 1 e 2, foram avaliados os impactos diretos e indiretos do fogo sobre vertebrados terrestres brasileiros, com base em dados obtidos pela Ciência Cidadã. Foram identificados os grupos taxonômicos mais negativamente impactados, os com maiores taxas de sobrevivência e os serviços ecossistêmicos prestados. Os resultados demonstram que vertebrados de pequeno porte (<1kg), especialmente répteis (59,1%), são os mais vulneráveis. Mamíferos (28,2%) também são impactados, comprometendo serviços ecossistêmicos cruciais, como sentinela de doenças, dispersão de sementes, ecoturismo e outros. Os vertebrados maiores (>7 kg) foram os que apresentaram maior sobrevivência. Espécies como Ozotoceros bezoarticus, Rhea americana, aves, Didelphidae, Myrmecophaga tridactyla e Chelonoidis sp. destacam-se entre as que apresentam maior probabilidade de sobrevivência, além de contribuírem para o serviço de dispersão de sementes. No Capítulo 3, foram estimadas a quantidade de aberturas subterrâneas que a fauna pode utilizar como refúgio contra o fogo em ambientes campestres do Parque Nacional da Serra da Canastra. Essas estimativas indicam cerca de 280,70 aberturas por hectares, que possuem equilíbrio térmico quando a temperatura externa se encontra muito alta, devido ao calor das chamas. Assim, os resultados desta dissertação contribuem para o entendimento da ecologia do fogo e das interações entre fauna e fogo em biomas brasileiros. Além de oferecer subsídios importantes para a conservação da biodiversidade e manejo do fogo, reforçando que queimas prescritas bem planejadas, que criam heterogeneidade ambiental e mantêm refúgios subterrâneos, são ferramentas valiosas para minimizar impactos negativos sobre a fauna e manter os serviços ecossistêmicos que essas espécies prestam.

Palavras-chave: impactos do fogo; ecologia do fogo; queimas prescritas; incêndio; fauna; Brasil

SUMMARY

1 GENERAL INTRODUCTION

Fire Ecology, the study of fire as an ecosystem process (KOBZIAR et al., 2024), is driven by both scientific interest in understanding the effects of fire on plants and animals and by the need for more effective fire management and sustainable vegetation practices (REGO et al., 2021a). Fire is an integral part of Earth's evolutionary history (SCOTT & GLASSPOOL, 2006). Following the emergence of humans, especially after they gained control over fire, its use intensified, affecting ecosystem structure and leading to profound landscape modifications, such as the creation of vegetation mosaics and the promotion of grasslands (PAUSAS & KEELEY, 2009). Consequently, fire is considered an ecological process that has shaped ecosystems, species, landscapes, and particularly, biodiversity (BOWMAN et al., 2009; HE et al., 2019).

Pyne (2021) proposes that we are living in a new geological era defined by fire, the Pyrocene, characterized by the increased use of fire, especially that derived from fossil fuel combustion. This era has triggered a global environmental crisis, marked by climate change and ecosystem degradation (DÍAZ et al., 2019; KECK et al., 2025). Droughts and heatwaves associated with these changes have altered ignition patterns and fuel structures (PAUSAS & KEELEY, 2021), increasing fire frequency and intensity (WU et al., 2021), and thereby generating megafires (MARENGO et al., 2021). Thus, although fire is an important ecological disturbance, large-scale wildfires increasingly pose a threat to ecosystems (DOS SANTOS et al., 2025), while also directly impacting public health, agriculture, and biodiversity, resulting in substantial economic losses (SOBREIRA et al., 2025).

According to Hardesty et al. (2005), the world's biomes can be classified as fire-sensitive, fire-dependent/influenced, and fire-independent, based on natural ecosystems and fire regimes. Natural fire regimes comprise: i) temporal characteristics, such as fire frequency and seasonality; ii) spatial characteristics, including burned area, fire size, and patch size distribution; and iii) magnitude, such as fire severity and intensity (REGO et al., 2021b). Brazil encompasses diverse ecosystems, including humid tropical forests such as the Amazon and the Atlantic Forest, where fire impacts are particularly severe due to the lack of fire-adaptive traits in most plant and animal species, classifying these ecosystems as fire-sensitive (BRANDO et al., 2014; PIVELLO et al., 2021). Grassland and savanna environments, such as the Cerrado, Pantanal, and Pampa, coevolved with fire, and their flora and fauna exhibit a range of adaptations and synergistic interactions with fire, making them ecologically fire-dependent (PIVELLO et al., 2021). In contrast, the Caatinga, a semi-arid ecosystem, rarely experiences fire, either due to unfavorable climatic conditions or a lack of fuel continuity to support fire spread (PIVELLO et al., 2021).

Fire affects animals at three different levels, which roughly correspond to: i) direct effects, also called first-order effects, which occur over a short period and involve mortality or injury; ii) indirect effects, or second-order effects, which occur in the long term, especially through habitat alterations; and iii) evolutionary effects of fire on animals, where fire regimes can drive adaptive changes in species over time (WHELAN et al., 2002; ENGSTROM, 2010). However, these effects depend on the ecological characteristics of species, as well as their morphological and behavioral traits, evolutionary exposure to fire, environmental factors (such as fuel loads and moisture), and fire behavior (WHELAN et al., 2002; BANKS et al., 2017; PAUSAS & PARR, 2018; NIEMAN et al., 2021; GONZÁLEZ et al., 2022; POCKNEE et al., 2023; SOUZA et al., 2023; HARMANGE et al., 2024).

Direct fire effects on animals pose an immediate threat (LEWIS, 2020). As fire spreads across the landscape, animals that remain within the burn perimeter die if they cannot escape or find adequate shelter (NIMMO et al., 2019; JOLLY et al., 2022). These effects include deaths caused by burns, smoke inhalation, desiccation, and physiological stress (NIMMO et al., 2021; MICHEL et al., 2023; BATISTA et al., 2023). Fires of high severity and intensity cause extensive animal mortality (PAUSAS & PARR, 2018; JOLLY et al., 2022). In the Brazilian Pantanal in 2020, approximately 17 million vertebrates are estimated to have been killed directly by fire (TOMAS et al., 2021). Widespread mortality has also been documented in the Chiquitania Forest of Bolivia, with 5.9 million mammals dying during the 2019 fires (PACHECO et al., 2021), and in Australia, during the 2019–2020 wildfires, with estimates of more than one billion animals killed (LEWIS, 2020).

Survival during the fire is not the only challenge animals face (ENGSTROM, 2010). Fire can significantly alter both habitat and habitat use by animals (REGO et al., 2021a). Survivors may face food and shelter scarcity and increased vulnerability to predation after fire (DOHERTY et al., 2022; MAGIOLI et al., 2024). Thus, the indirect effects of fire influence long-term population viability because landscapes change as vegetation responds to fire effects (REGO et al., 2021a).

Additionally, animals may recolonize burned areas immediately or shortly after fires, and many species can thrive in recently burned landscapes (REGO et al., 2021a). Opportunistic species, such as herbivores, large predators, scavengers, and granivores, may have foraging facilitated and are thus recognized as fire-adapted fauna (PAUSAS & PARR, 2018). This is due, for example, to increased resource availability, including grass and leaf regrowth, fleeing prey, or carrion (NEWSOME & SPENCER, 2021; THAPA et al., 2022; DOHERTY et al., 2022; MAGIOLI et al., 2024). In Australia, three species of raptors are known to intentionally ignite fires by carrying burning sticks into unburned areas to hunt (BONTA et al., 2017).

The behavior of fire-spreading raptors to catch prey indicates that these species are adapted to respond to fire in fire-prone ecosystems (DOHERTY et al., 2022). In contrast, other species may develop or enhance behaviors to detect and rapidly flee fires, which also confers an adaptation, as direct fire impacts are often harmful to animals (PAUSAS & PARR, 2018). Thus, fire likely acts as a selective pressure on many of these behaviors, similarly to other enemy-driven selective pressures, such as predation (PALMER & PACKER, 2021).

These behaviors include the ability to recognize olfactory, auditory, and visual fire cues, eliciting protective responses that can enhance survival (NIMMO et al., 2021; JOLLY et al., 2022). In Ivory Coast, researchers documented that some individuals of a frog species can recognize the sound of fire and quickly move toward habitats with protective cover (GRAFE et al., 2002). In the United States, lizards have been shown to detect smoke compounds by flicking and retracting their tongues, which triggers escape behaviors (MENDYK et al., 2020). In Australia, trials with an opossum species revealed that individuals could detect smoke during torpor, wake up, and flee to a safer location (NOWACK et al., 2016).

In this regard, Nimmo et al. (2021) noted that many animals may seek non-flammable refuges, such as burrows, deep crevices, water bodies, and areas with less fire-prone vegetation. In Brazil, lizards and many other animals have been observed leaving underground refuges immediately after fire passage (COSTA et al., 2013; SEMEDO et al., 2022). Hence, animal survival depends on the degree of refuge protection, the animals’ mobility, and their morphological traits (BATISTA et al., 2023). Moreover, fire regimes are an important evolutionary agent in terrestrial animals, and changes in these regimes, along with the capacity for rapid evolution in wild animal populations, suggest the potential for fire-driven adaptive evolution in animals (JONES et al., 2023).

While research on the evolution of fire-prone ecosystems has historically focused on plants, new opportunities exist to examine fire–fauna interactions from an evolutionary perspective (PAUSAS & PARR, 2018). Accordingly, we aim to understand how fire affects vertebrate communities in Brazil, considering its direct, indirect, and evolutionary effects, in order to support informed decision-making for fire management and ecosystem stewardship across Brazilian biomes.

This dissertation was structured as a collection of scientific articles, with the formatting of the text, citations, and references conforming to the guidelines of each target journal. Consequently, some information presented in the general introduction is also repeated in the chapters where necessary. Chapter I addresses the ecological implications of the direct effects of fire, especially mortality, on Brazilian terrestrial vertebrates. This article was entirely supported by a Citizen Science approach, using voluntarily submitted images from firefighters, brigadistas, researchers, and local community members who documented fire suppression and prescribed burns across Brazil. Chapter II, also based on the same Citizen Science methodology as the previous chapter, examines the indirect effects of fire on vertebrates, with a focus on understanding both their survival and how these effects may alter their behavior. Finally, Chapter III discusses how the availability of underground refuge openings influences animal survival in Serra da Canastra National Park, Minas Gerais.

2 OBJECTIVES

2.1 General objective

To investigate the impacts of fire on wildlife in Brazil by identifying the most affected taxonomic groups, the survival strategies they adopt, with emphasis on the use of underground refuges, and the ecosystem services compromised, in order to understand the patterns of vulnerability and resilience of animals in the face of wildfires.

2.2 Specific objectives

Chapter 1:

- Assess the taxonomic groups most negatively impacted;
- Identify the ecosystem services provided by mammals negatively affected by fire;

Chapter 2:

- Analyze the surviving taxonomic groups and their body sizes;
- Identify potential behavioral survival strategies;
- Determine which taxa have the highest probability of survival.

Chapter 3:

- Estimate the amount that fauna can use as protection against fire in the grassland environments of the Serra da Canastra National Park;
- Infer which animals are capable of using these shelters, considering their habits;
- Evaluate the change in temperature inside the shelters during the passage of fire.

CHAPTER 1

Ecological implications of the direct effects of fire on neotropical vertebrates

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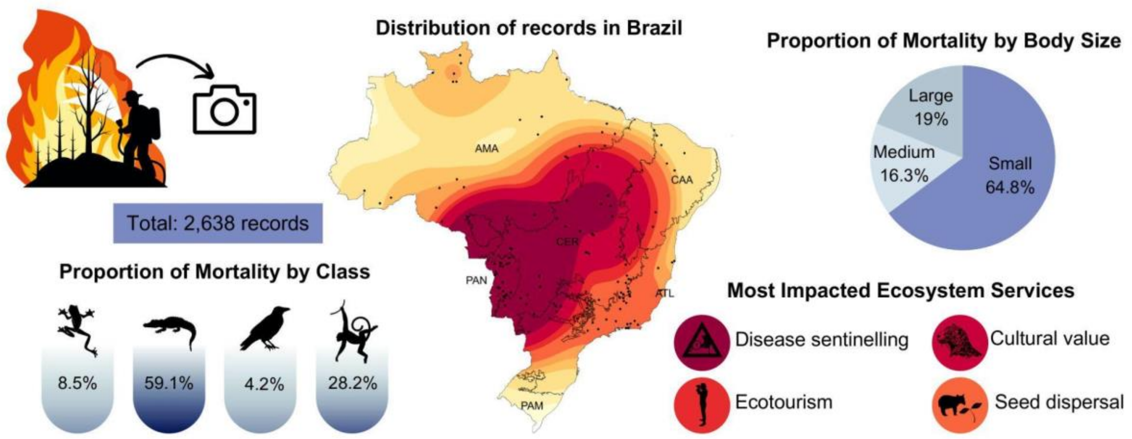
Article published in the Journal *Science of The Total Environment.*

Consultation available at: https://doi.org/10.1016/j.scitotenv.2025.179437

Highlights:

- Vertebrates weighing <1 kg suffer the highest mortality in Brazil's fires;
- Reptiles were the group with the highest mortality recorded (59.1 %);
- Mammals, amphibians and birds represented 28.2 %, 8.5 % and 4.2 % respectively;
- Disease sentinelling is the most impacted ecosystem service provided by mammals;
- Our citizen science data focused mainly on the Brazilian Pantanal region.

Graphical Abstract:



Abstract: Changes in fire regimes have significantly impacted wildlife, affecting both mortality rates and indirect effects on fauna. Estimating the direct effects of fire on animals is complex and variable, revealing a knowledge gap regarding animal mortality and the consequent loss of ecosystem services. To address this gap, we conducted an analysis to identify the taxonomic groups most negatively affected by fire and to assess the ecosystem services provided by impacted mammals. We utilized a Citizen Science-based database containing photographs of animals directly affected by fire in Brazil. Our dataset includes 2,638 individuals distributed across five of the six Brazilian biomes. Our results indicate that reptiles were the most affected group (59.02%), followed by mammals (28.20%). Among the most compromised ecosystem services are disease sentinelling, the cultural value of charismatic species, ecotourism, and seed dispersal. Additionally, we confirmed the hypothesis that small-bodied and low-mobility animals are the most vulnerable, accounting for 64.78% of the records. Finally, we recommend strategies to mitigate the negative effects of fire on wildlife and to enhance the understanding of these impacts, such as biodiversity monitoring using genetic methodologies.

Keywords: Wildfire; Prescribed burning; Fauna; First-order effect; Ecosystem services; Brazil.

1. Introduction

Fire acts as a modulating agent of landscapes, biodiversity, and the dynamics of socioecological systems, playing a key role in various ecosystems worldwide (Bowman et al., 2009; McLauchlan et al., 2020). However, fire regimes are influenced by specific climatic conditions and anthropic activities (Fonseca et al., 2017; Stephens et al., 2018; 2020; Lindenmayer et al., 2020; Duane et al., 2021), which increases extinction risks for many species (Kelly et al., 2020). Furthermore, changes in fire regimes, accelerated environmental changes and the ongoing loss of global biodiversity can undermine ecosystem stability (Bowman et al., 2020), changing the functions and ecosystem services provided (Oliver et al., 2015; Tourinho et al., 2025).

The effects of fire on fauna can vary depending on the species (Souza et al., 2023; Harmange et al., 2024; Ribeiro et al., 2025) according to their morphological, behavioral, and ecological traits (Nieman et al., 2021; Pocknee et al., 2023). These effects are classified as direct (first-order), indirect (second-order), and those related to the historical evolution of fire (third-order) (Engstrom, 2010). Direct effects include deaths caused by burns, smoke inhalation, desiccation, and physiological stress (Nimmo et al., 2019; 2021; Jolly et al., 2022; Michel et al., 2023; Batista et al., 2023), as occurred in Brazil's Pantanal in 2020, where an estimated 17 million vertebrates died (Tomas et al., 2021); in Bolivia's Chiquitano Forest during the 2019 wildfires, where mammal deaths were estimated at 5.9 million (Pacheco et al.,2021); and in Australia during the 2019-2020 wildfires, with estimates suggesting that over one billion animals perished (Lewis, 2020).

These wildfires that occurred in Brazil's Pantanal in 2020 are considered the largest, most complex, and most severe in recorded Brazilian history. Consequently, considerable effort was invested in understanding their effects and devising more efficient prevention measures. In this regard, Magioli et al. (2024) demonstrated that although no local extinctions were observed, the fires resulted in an abrupt reduction in the abundance of all medium- and large-sized mammal species, showing concern about recurring similar events.

From this perspective, fire can stimulate the development of strategies and adaptations that enable animals to recognize olfactory, auditory, and visual cues of fire, promoting the adoption of escape behaviors (Nimmo et al., 2021), such as moving to unburned areas or using refuges (Pausas, 2019; Pausas & Parr, 2018), particularly in regions with recurring fires. However, indirectly, animals may be hit by vehicles while fleeing from fire (Lacet et al., 2023); in the medium and long term, they may experience changes in habitat structure and resource availability (Swan et al., 2015; González et al., 2022), increased predation rates (Robinson et al., 2013; Michel et al., 2023; Batista et al., 2023), and reduced abundance rates (Magioli et al., 2024). Additionally, fire can alter community composition, leading to consequent effects on ecological functions (Santos et al., 2022a, b; Magioli et al., 2024).

Despite its negative impacts, fire can generate positive effects in certain ecological contexts, considering the variability in responses among different species and ecosystems. Studies highlight that fire promotes the diversity and abundance of some species, particularly in fire-adapted ecosystems, creating favorable conditions for recolonization and resource availability (González et al., 2021; Costa et al., 2022; González et al., 2022; Moritz et al., 2023).

Estimating the direct effects of fire on fauna is complex and highly variable, due to species-specific responses, behavioral adaptations, and variability in fire characteristics (Pausas & Parr, 2018). In this context, studies aiming to understand the effects of fire on fauna and the maintenance of ecosystem services remain scarce, particularly in Brazil (Jolly et al., 2022; Berlinck et al., 2021).

To enhance knowledge about the effects of fire on fauna in Brazil and strengthen conservation efforts, we aim, with the support of Citizen Science i) assess the taxonomic groups most negatively impacted and ii) identify the ecosystem services provided by mammals affected by fire. We hypothesize that small-bodied animals with low mobility are the most severely impacted, leading to changes in the ecosystem services they provide.

2. Material and methods

2.1. Building a database

A database was created using images voluntarily submitted by firefighters, employees of Brazilian environmental agencies, and researchers involved in monitoring firefighting and prescribed burning in Brazil. These data were received by the National Research and Conservation Center for Carnivorous Mammals (CENAP), part of the Chico Mendes Institute for Biodiversity Conservation (ICMBio), and included photographs of vertebrates directly impacted by fire. Additionally, databases provided by the non-governmental organization (NGO) Onçafari and the Wild Animal Rehabilitation Center (CRAS) of the State of Mato Grosso do Sul (MS) were included, as well as three databases published by partners (available in Tomas et al., 2021; Brack et al., 2024; de França Gomes, 2024), and photographs collected from online news sources displaying such information. Images recorded between 1998 and 2024 were considered.

The photographs were organized in a Microsoft Excel spreadsheet, where each row represented an animal impacted by fire. We also compiled: i) biome, ii) state, iii) location or name of the Protected Area, iv) fire event, v) class, vi) order, vii) family, viii) genus, ix) species, and x) body size. Animals were classified into three body size categories: small (less than 1 kg), medium (between 1 kg and 7 kg), and large (greater than 7 kg) (Emmons & Feer, 1997; Chiarello, 2000), based on the average weight of the species. The fire regime classification was divided into wildfire and prescribed burning.

We used the definitions of Pivello et al. (2021) to classify the fire regime of each record, dividing them into wildfires and prescribed burning. A wildfire is an unplanned, uncontrolled fire, usually caused by lightning or human activity. In contrast, a prescribed burn is a controlled, planned fire, within a defined area and conducted based on management objectives. Wildfires can be classified into three types based on their behavior and the fuel they consume: (i) underground wildfires, which burn organic material below the surface, such as peat and humus, often smoldering for long periods and considered the most severe fire; (ii) surface fires, which spread through leaf litter, grasses, and shrubs, are capable of damaging vegetation and wildlife; and (iii) crown fires, which reach the canopy, spreading rapidly through tree crowns and causing severe ecological impacts (Torres et al., 2020). Regarding the characterization of biomes, Table 1 presents the analyzed biomes, their main landscape characteristics, and their relationship with fire.

Whenever possible, animals were identified to the species level; in cases where exact identification was not feasible, at least the order to which they belonged was determined. Visual criteria, such as the visibility of key body parts, were used for species identification. Expert researchers were consulted to achieve the smallest possible taxonomic group.

Table 1: Biomes analyzed, their main landscape characteristics, and their relationship with fire. This table was developed based on Pivello et al. (2021).

Biome	Relationship of fire
Cerrado, Pantanal and Pampa	fire-dependent; open vegetation (grasslands, open savannas)
Amazon basin and Atlantic Forest	fire-sensitive; forests (rainforests, seasonal forests, woodland savanna)
Caatinga	fire-independent; xerophytic vegetation

2.2. Data analysis

A total of 2,650 records of animals were obtained, but to correct biases in data estimates a data filtering process was applied for the analyses (Kamp et al., 2016), 12 records lacking initial class identification were excluded from the analyses. All analyses were performed using R software (v 4.4.1 R Core Team, 2024).

To illustrate the distribution patterns of the received photographs, a Kernel density estimation analysis was conducted using QGIS software (version 3.38.3). Centroids were established based on the geographic coordinates of the recording locations for the density estimation. In cases where the exact location of the photograph was unavailable, the general centroid coordinate of the state and/or biome of origin was used.

A multivariate analysis was conducted using Multiple Correspondence Analysis (MCA), which allowed for the reduction of data complexity and the representation of categorical data patterns considering both the biome and the fire event (wildfire or prescribed burn), the class, and the body size of the animals.

To assess the impact of fire on the ecosystem services (ES) provided by mammals, we used the classification proposed by Vale et al. (2023). From the supplementary material of this study, we extracted the list of mammalian orders and their associated ES. We then compiled a list of the mammalian orders recorded in our dataset, along with the sample size for each order, represented by the number of individuals found dead. Cross-referencing these data, we determined the affected ES based on the species composition and abundance of fire-related mortality within each order.

For the mammalian species that we were able to identify, we applied the same approach at the species level, linking each species to the ES described by Vale et al. (2023). This allowed us to quantify the extent to which different ES were impacted by fire, based on the observed mortality patterns in our dataset.

The identified ES were: (i) cultural service charismatic species (species with cultural or symbolic importance, often valued for conservation) and (ii) ecotourism (species that attract visitors and contribute to local economies); (iii) pollination (the transfer of pollen by animals), (iv) seed dispersal (the movement of seeds by animals, aiding in plant regeneration), (v) pest and disease control (reduction of agricultural pests and disease vectors), (vi) rodent control (rodent predation and regulation, helping to prevent outbreaks) and (vii) disease sentinelling (species that indicate the presence of pathogens in the environment, helping monitor disease risks); (viii) carrion control (scavenging activity that accelerates decomposition and nutrient cycling), (ix) nutrient transporting (movement of nutrients on ecosystems), (x) top-down regulation (predator-prey interactions that help maintain ecological balance), and (xi) ecosystem engineering (modification of habitats by species which influences ecosystem structure).

2.3. Sampling effort

We used the FreScaLO algorithm (Frequency Scaling using Local Occupancy, hereafter referred to as "Frescalo") (Hill, 2012) to model data and correct spatial and temporal discrepancies associated with Citizen Science-based data collection. Although this approach provides a valuable source of global, unstructured biodiversity data (Kosmala et al., 2016; Chandler et al., 2017; Bonney, 2021; Callaghan et al., 2024; Mandeville et al., 2023), heterogeneity in sampling effort, climatic conditions, and observer profiles (Johnston et al., 2019) compromise the understanding of species distributions (Callaghan et al., 2024). These limitations are accentuated in records made by firefighters, for being subject to stress, extreme heat, and fatigue (Jeklin et al., 2020; Fullagar et al., 2021). Additionally, the heterogeneous distribution of collaborators and the complexity of firefighting actions in Brazil result in unmonitored wildfires, impairing the representativeness of the collected data.

Frescalo (Hill, 2012) was implemented in the Sparta package (v0.2.19 August et al., 2015) in R (v 4.4.1 R Core Team, 2024) and performs well with Citizen Science data (Isaac et al., 2014), enhancing the estimation of trends and species occurrence in under-sampled areas (Dyer et al., 2016; Pescott et al., 2022). It evaluates the recorder's effort by comparing observed species with those expected in nearby regions with similar ecological composition, calculating standardized local species frequencies based on geographic distance and landscape similarity (Hill, 2012). Landscape similarity was assessed using biome classification. For records without species-level identification, the next available taxon was considered.

According to Frescalo results, the TFactor was used as a relative measure to assess the temporal frequency of species occurrence, indicating their relative probability of being recorded over time. For this analysis, species with low uncertainty in frequency estimates (StDev < 1) and high TFactor values (> 1) were selected, suggesting a higher probability of the species being found broadly and consistently over time.

3. Results

This research represents the first study found in the literature utilizing Citizen Science to document animals directly impacted by fire through photographic records. A total of 2,638 records of animals were obtained, distributed across five of Brazil’s six terrestrial biomes over 26 years (1998–2024). These results revealed that 65.84% of all records were concentrated in the Pantanal biome (1,737), followed by 21.19% in the Cerrado (559), 7.08% in the Amazon (187), 4.96% in the Atlantic Forest (131), and 0.9% in the Caatinga (24), with no records from the Pampa biome (Fig. 1). A total of 1,202 animals (45.56%) were recorded within Protected Areas (PAs), including Conservation Units and Indigenous Lands, while 414 records (15.69%) were from privately PAs. Fire event data indicated that 84.6% of the records were from wildfires (2,232) and 15.39% from prescribed burns (406).

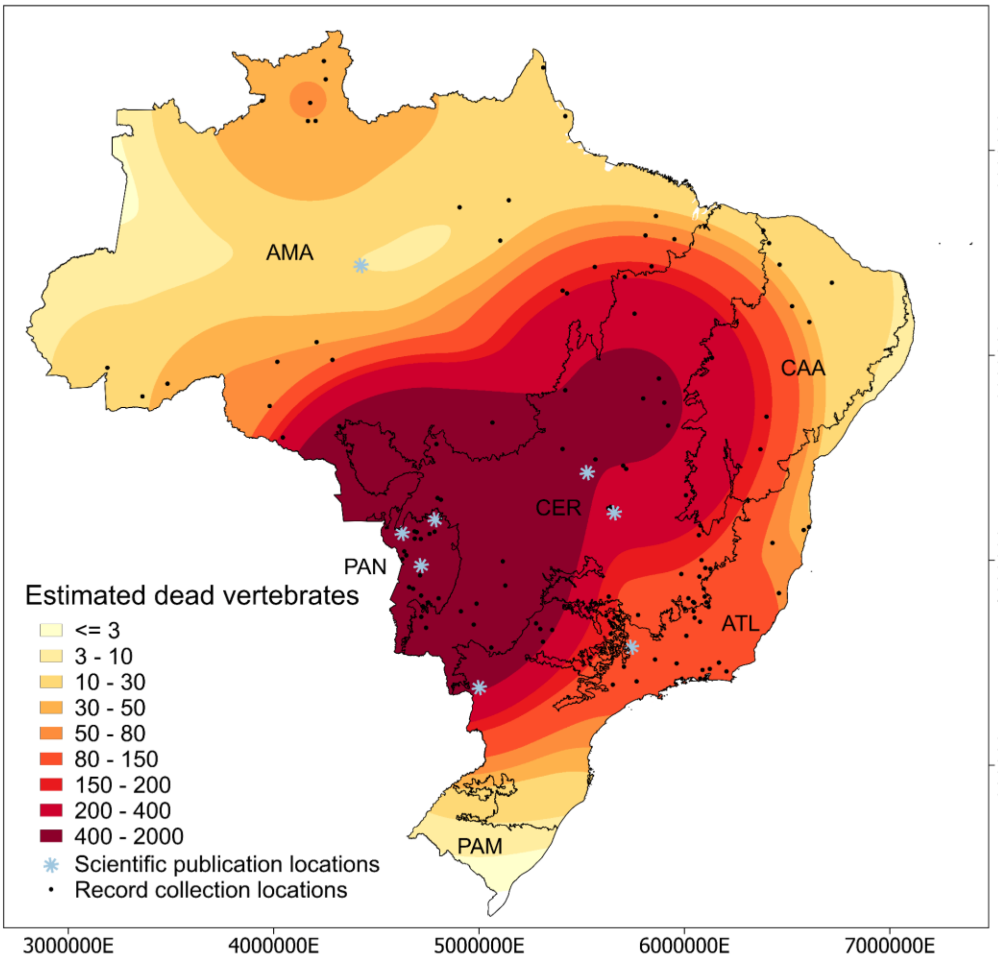


Fig. 1: Spatial distribution of the density of records of direct effects of fire on Brazilian wildlife. Black lines indicate biome boundaries: AMA – Amazon, ATL – Atlantic Forest, CAA – Caatinga, CER – Cerrado, PAM – Pampa, and PAN – Pantanal. Asterisks denote locations with published studies on the direct impacts of fire.

The MCA revealed significant patterns in the relationships among biomes, fire events, and taxonomic groups, while also considering animal body size, describing a total of 58.23% of the data variance and indicating dispersion. Dimension 1 (Dim 1) highlighted marked differences between biomes, where the Cerrado was directly associated with prescribed burns, the Pantanal with wildfires, and the Caatinga showed an opposing contribution. Dimension 2 (Dim 2) revealed a clear separation among taxonomic groups, with amphibians occupying a distinct position relative to reptiles and mammals. Prescribed burns and wildfires played opposing roles in shaping the axes, emphasizing that these fire types impact species differently. Prescribed burns and the Cerrado showed a low correlation with the other data (Fig. 2). The results indicate that fire impacts vary according to the biome, taxonomic characteristics of the species, and particularly, the fire event type. Regarding animal body size, and revealing an alarming impact on small vertebrates, 64.78% of the records involved small-bodied animals

(1,709), including amphibians (13.16%, 225 records), reptiles (76.12%, 1,301 records), birds (4.85%, 83 records), and mammals (5.85%, 100 records). 16.26% medium-bodied animals (429), and 18.95% large-bodied animals (500).

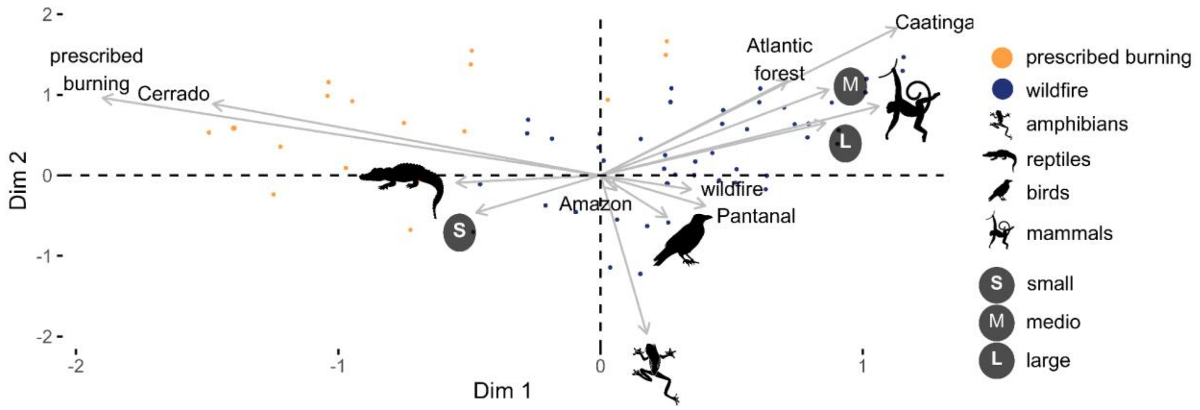


Fig. 2: Description of groups negatively impacted by fires obtained from a Multiple Correspondence Analysis (MCA). (Dim 1: Dimension 1, Dim 2: Dimension 2).

Amphibian (225) and reptile (1,557) records accounted for 67.55% of the total, distributed among snakes (859), lizards (558), turtles (58), caimans (82), and frogs (223). Gymnophthalmidae was the family with the highest number of identified records (198) for lizards, followed by Scincidae (60). Among snakes, Dipsadidae (93) and Colubridae (83) were the most representative families. Among squamates, 853 records could not be identified to the species level due to the condition of the recorded carcasses (see example in Figure 3D); however, 594 were identified as snakes and 259 as lizards. Birds accounted for 4.24% of the records (112), with the Galliformes (13) and Columbiformes (8) orders being the most represented. Additionally, 42 bird records could not be identified due to the same challenges faced with squamates. Fig. 3 provides examples of photographs of animals recorded in this study.

Fig. 3: Photographs of animal carcasses. A) Anuran in the 2020 wildfire in Pantanal; B) Sloth in the 2024 wildfire in Atlantic Forest; C) Chelonians in the 2024 wildfire in Bananal Island/TO; D) Snake in the 2024 wildfire in Pantanal; E) Alligator in the 2024 wildfire in Pantanal; and F) Rodent in the 2023 wildfire in Pantanal (Source: CENAP/ICMBio Collection).

Mammals accounted for 28.20% of the records (744), with notable representation from the orders Rodentia (239) and Artiodactyla (179). In Fig. 4, which outlines the ecosystem services (ES) according to Vale et al. (2023), it is evident that records of deceased mammals include representatives in all 11 types of ES. Rodentia and Carnivora stand out for providing eight ES each, while Artiodactyla contributed to six ES.

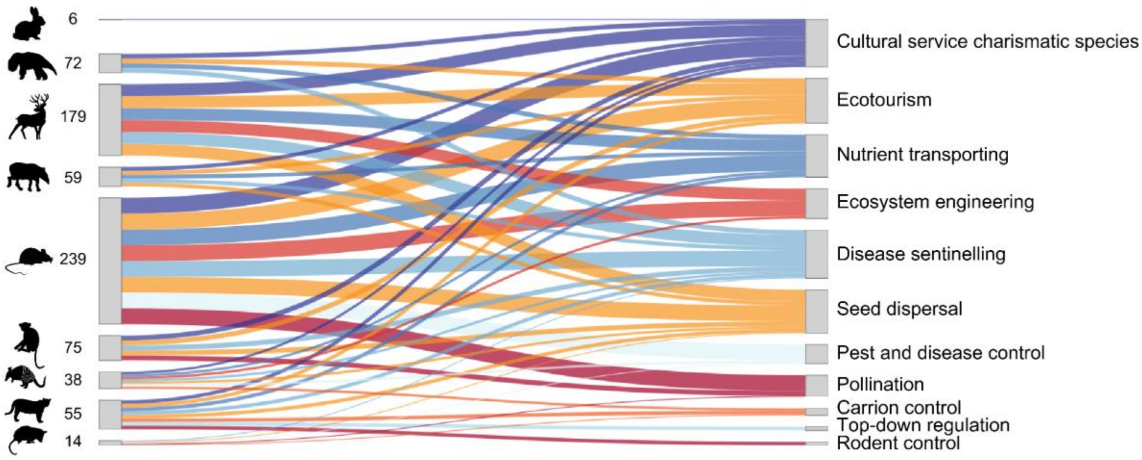
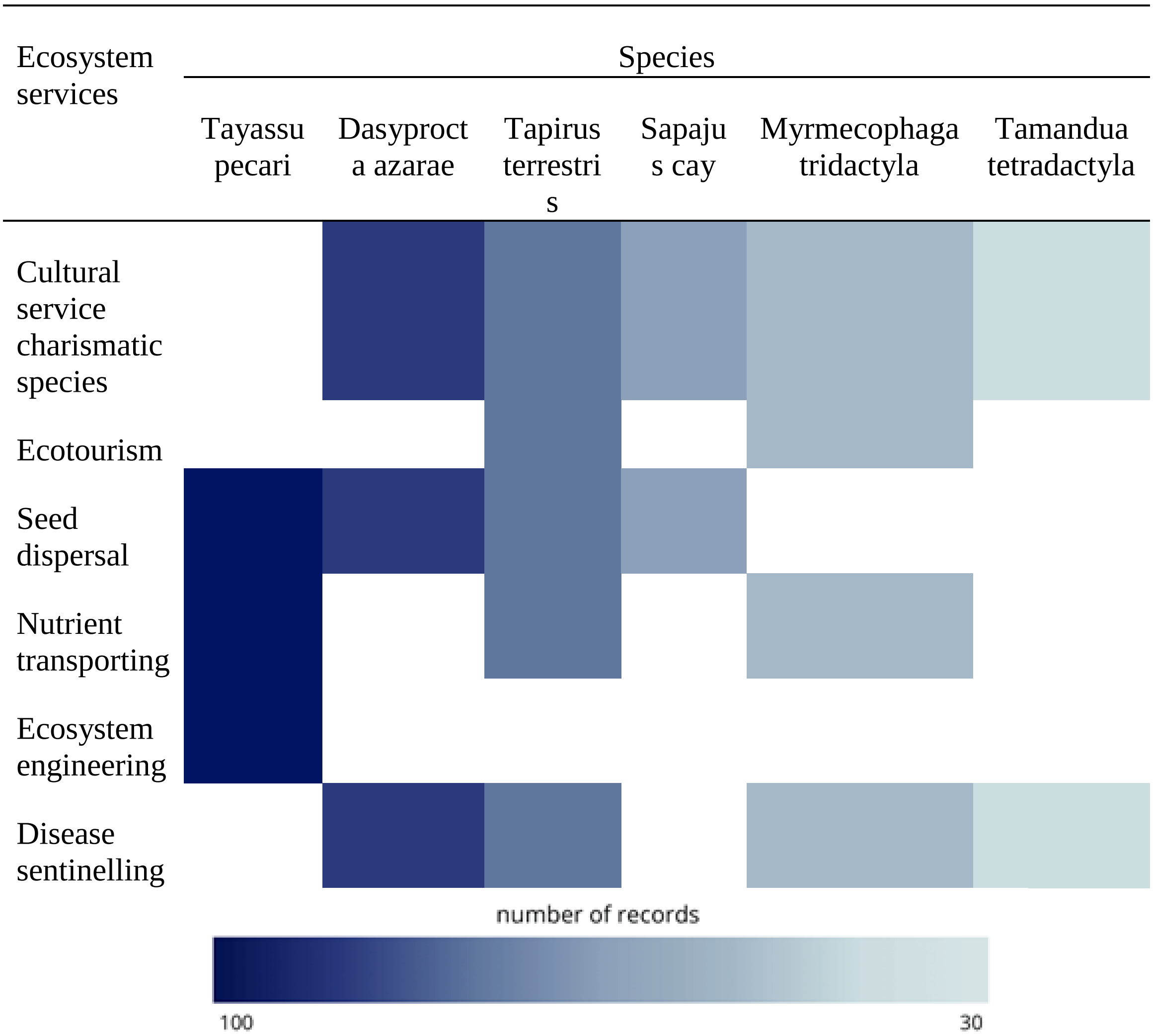


Fig. 4: Number of records of dead mammals, by order, and their correlation with the ecosystem services provided. On the left axis, the orders are: Lagomorpha, Pilosa, Artiodactyla,

Perissodactyla, Rodentia, Primates, Cingulata, Carnivora and Didelphimorphia.

A total of 544 mammal records were identified at the species level, with notable highlights including *Tayassu pecari* (95), recognized as a seed disperser, nutrient transporter, and ecosystem engineer; *Dasyprocta azarae* (65), valued for its cultural and charismatic significance, seed dispersal, and role as a disease sentinel; *Tapirus terrestris* (57), a charismatic species essential for ecotourism, nutrient transport, seed dispersal, and disease sentinel functions; *Sapajus cay* (43), both charismatic and a key seed disperser; *Myrmecophaga tridactyla* (30), notable for its charismatic value, ecotourism importance, nutrient transport, and disease sentinel role; and *Tamandua tetradactyla* (26), recognized for its charismatic significance as well as its role as a disease sentinel (Table 2).

Table 2: Mammal species with the highest number of identified records and their respective ecosystem services. The color scale reflects the frequency of records, with darker tones associated with species with more records and lighter tones with fewer records.



Our analysis using the Frescalo method identified 12 species or taxonomic groups with a high relative frequency of temporal occurrence and low uncertainty in the records. Among them, snakes, with TFactor 4.219, and lizards (2.244), were particularly frequent, as well as the species *Myrmecophaga tridactyla* (1.829) and *Cuniculus paca* (1.452). Additionally, the order Rodentia was notable for its significant contribution to ecosystem services, while *Dasypus novemcinctus* stood out for providing seven different types of ecosystem services (Fig. 5).

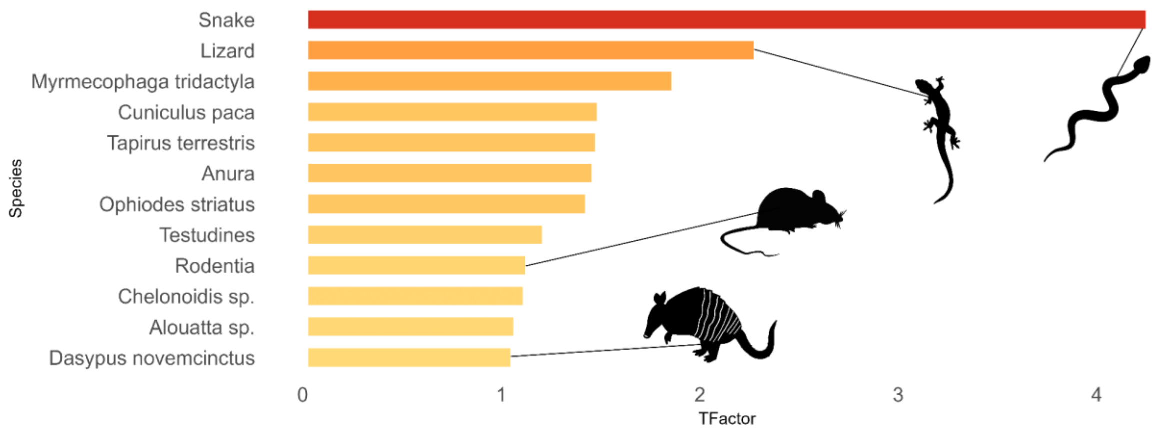


Fig. 5: Taxonomic groups with significant TFactor (> 1) and low uncertainty (StDev <1), with emphasis on snakes, lizards, rodents and Dasypus novemcinctus. TFactor corresponds to the estimated relative frequency of species. The analysis presented considers different taxonomic levels due to the identification available in each record, opting for the higher taxonomic level when specific identification was not possible.

In the analyzed records, we observed that only 1% corresponded to live animals with burns, while the remaining referred to deceased animals. Due to this significant difference, we opted to use the term "mortality" throughout the text to broadly and representatively encompass the data.

4. Discussion

In this study, we hypothesized that small-bodied animals with low mobility would be the most severely impacted by fire, leading to significant changes in the ecosystem services they provide. We accept this hypothesis based on our findings, which show that these animals were particularly vulnerable to fire-induced mortality. Biodiversity is essential for the long-term resilience of ecosystem services and the ecological functions they support (Pecl et al., 2017). Therefore, the loss of these species could disrupt critical ecological functions, further compromising the resilience of ecosystems. In the following sections, we discuss the direct effects of fire on different biomes and species, focusing on how these impacts align with our hypothesis and their implications for ecosystem services.

4.1. Biomes, habitats and ecological resilience

The analyses from this study revealed that most records were concentrated in the Pantanal biome. The Pantanal is the largest continental wetland in the world (Couto et al., 2023), which has faced a high degree of threat in recent years due to extreme droughts (Ribeiro et al., 2022). Especially, for the recent changes in human activities, such as increased land conversion and unsustainable agricultural practices, including extensive livestock grazing, and ineffective enforcement of environmental laws, have significantly increased the vulnerability of the Pantanal to wildfires (Libonati et al., 2020).

A complex interaction of meteorological/climatic, landscape, and human factors (Garcia et al., 2021), combined with inadequate fire management (Libonati et al., 2020), resulted in the largest wildfires ever recorded in the biome in 2020 (Pelissari et al., 2023), with 43% of the affected area burning for the first time in at least 20 years (Martins et al., 2022). As a consequence, underground wildfires occurred, representing one of the greatest challenges for firefighters during those events (Damasceno-Junior et al., 2021).

In general, like other Brazilian grassland environments such as the Cerrado and Pampa, the Pantanal is also a fire-prone biome from an ecological perspective (Pivello et al., 2021), where fire historically played a role in creating and maintaining mosaics, acting as a fundamental element for local ecological dynamics (dos Santos Ferreira et al., 2023). However, physical, climatic, and anthropogenic variables directly influence the incidence and spread of fire, making these areas more vulnerable to large wildfires in Brazil (Oliveira et al., 2023).

For the Cerrado, there are more records of prescribed burns than wildfires, which can be explained by several factors. Prescribed burning is a planned action implemented in various PAs within the biome, where monitoring is more accessible (Schmidt et al., 2018), and it is widely employed in the Cerrado, the first biome to implement it as a preventive measure. In the Pantanal, prescribed burns were initially conducted on a small scale in 2021 as pilot tests. Compared to the Pantanal, the direct effects of fire in the Cerrado are less intense, because fires occur more frequently due to the pyrocognition (Jacobs, 2020; Jacobs et al., 2022), evolutionary adaptations and strategies of species in fire-prone habitats (Jolly et al., 2022). In these areas, mortality rates are lower compared to rarely burned environments, and proper fire management can even lead to increased animal richness and abundance (Durigan et al., 2020; Ensbey et al., 2023). This difference reflects evolutionary selection that has favored survival mechanisms, such as the ability to recognize signs of imminent fires and adopt adaptive behaviors (Nimmo et al., 2021; Pausas & Parr, 2018), including the use of unburned refuges like burrows, soil cracks, and hollow logs (Robinson et al., 2013; McWethy et al., 2019; Bergstrom et al., 2023; Linley et al., 2024).

The differences in the number of records between the Pantanal and Cerrado may also be explained by animal population density, and also because in the Pantanal, surface fires, underground fires, and crown fires occur concurrently. The Pantanal is characterized by abundant wildlife, a consequence of its high primary productivity and the well-preserved condition of the ecosystems that comprise its floodplain (Tomas et al., 2019). Compared to the Cerrado, the Pantanal supports higher faunal densities but exhibits low endemism (Brown Jr., 1986; Rodrigues et al., 2002). Additionally, it harbors the highest density of mammal species per square kilometer in the world (Tomas et al., 2010). These findings may also reflect the increased attention given to the impacts of recent wildfires that have affected the biome (Pereira et al., 2024).

In contrast, tropical forests such as the Amazon and the Atlantic Forest are considered fire-sensitive ecosystems (Pivello et al., 2021). However, both have been increasingly affected by alterations in fire regimes driven by land use and land cover changes (Alencar et al., 2015; de Andrade et al., 2020). Over the past decades, wildfires have impacted Amazonian biodiversity, affecting numerous species already classified as threatened by the International Union for Conservation of Nature (IUCN) (Feng et al., 2021). It is expected that this impact will intensify as fires encroach upon the central Amazon Basin, which harbors the highest levels of biodiversity (Feng et al., 2021). Research indicates that wildfires affecting forests or disrupting forest connectivity can have negative consequences for mammals (Paemelaere et al., 2024), turtles, and agoutis, as well as cause the death of arboreal vertebrates by asphyxiation, including primates, sloths, and birds (Barlow & Silveira, 2009), given that few tropical forest species are adapted to fire (Oliveira et al., 2019).

The scarcity of data on the impact of wildfires and prescribed burns in the Caatinga, as well as the lack of information for the Pampa, may be attributed both to the limited monitoring efforts and the shortage of personnel available for such tasks, as well as to the potential absence of fire events. However, in this study and many other cases, records available in community-contributed databases represent the only existing information on biodiversity (Guillera-Arroita, 2017). While the lack of consolidated data poses a challenge for researchers, leading to repeated costs for similar studies (Guimarães et al., 2024), Citizen Science plays a crucial role in enabling large-scale data collection, facilitating approaches that would otherwise be logistically or financially unfeasible (Stuart-Smith et al., 2013), particularly in Brazil.

4.2. Direct Effects on Vertebrates

Previous studies suggest that small-bodied animals, which can more easily find refuge during wildfires (Mahony et al., 2022), large-bodied animals, which can escape or move away from affected areas (Griffiths & Brook, 2014), and species with short fur, smooth skin, or scales (Batista et al., 2023) exhibit lower fire vulnerability. Conversely, medium-sized animals face greater challenges in escaping or finding shelter (Griffiths & Brook, 2014), as well as species with long, coarse fur or feathers, are considered more vulnerable (Silveira et al., 1999; Batista et al., 2023).

However, the data presented here indicate that small-bodied and scaled animals are the most impacted by fire, a finding that contrasts with previously reported trends. This result aligns with mortality estimates from the 2020 megafires in the Pantanal, which led to the death of approximately 16 million small vertebrates (Tomas et al., 2021), and with a meta-analysis demonstrating a pronounced negative effect of wildfires on small vertebrate abundance (Giorgis et al., 2021), particularly among less mobile species, like the smaller reptiles (Griffiths & Brook, 2014; Mendonça et al., 2015; Tomassini & Massolo, 2024).

Reptiles were the group most severely impacted by fire. Compared to other animal groups, they experience the highest direct mortality rates from both wildfires (Tomas et al., 2021) and prescribed burns (Jordan et al., 2020). Currently, 14% of terrestrial reptiles are classified as threatened with extinction by the International Union for Conservation of Nature (IUCN), facing risks associated with altered fire regimes (Kelly et al., 2020; Santos et al., 2022b). In Australia, inappropriate fire regimes threaten 43% of conservation-priority squamates, where high fire intensity, severity, and frequency are the primary drivers of fire-related population declines (Santos et al., 2022b). Documenting fire-induced mortality is particularly challenging for small and cryptic animals, such as snakes and lizards (Smith et al., 2012). In this study, reptiles accounted for approximately 59% of the recorded negative impacts, but due to the condition of the carcasses in the analyzed images, species-level identification was often not possible. Therefore, while our data do not allow us to directly assess the conservation status of the affected species, the high proportion of reptile mortality observed highlights the potential risk to species already classified as threatened by the IUCN.

A study conducted in the Pantanal revealed that among herpetofauna groups, reptiles exhibited the highest number of species and mortality records. This pattern aligns with the high reptile diversity reported for the Pantanal herpetofauna, which surpasses that of amphibians. However, this finding contrasts with typical abundance data for the biome, where amphibians are generally more numerous than reptiles (Valencia-Zuleta et al., 2024). The higher mortality observed in reptiles may be influenced by their limited dispersal ability, strong habitat dependency, and high sensitivity to environmental disturbances (Russell et al., 1999). These traits can make them more vulnerable to fire-induced mortality, as they may have fewer opportunities to escape rapidly spreading fires or to recolonize burned areas after disturbance.

Amphibians had fewer recorded cases, which may be attributed to their habitat preferences, as they are typically associated with humid environments therefore less susceptible to fire (O et al., 2020; Ribeiro et al., 2025). No specific studies have been identified on the direct impacts of wildfires on amphibian mortality (Jolly et al., 2022). However, frogs may be considered vulnerable to fire, as aspects of their physiology and behavior are directly influenced by changes in temperature and humidity, which are often exacerbated by wildfires (McLauchlan et al., 2020). Furthermore, their limited dispersal ability constrains their capacity to escape during and after fire events (Anjos et al., 2024).

Poikilotherm of the reptiles may influence fire survival, reducing immediate mortality in some cases, through the variation of body temperature according to the ambient temperature (Bícego, 2020). However, this would be possible if the availability of effective shelters were a key determinant of survival. Studies report that lizards sheltering in burrows or termite nests survived the fire (Costa et al., 2013; Smith et al., 2012; Atkins et al. 2015; Gorissen et al., 2018), whereas species lacking such refuges may experience extensive mortality (Tomas et al., 2021; González-Fernández et al., 2024). This way, while the thermoregulatory strategies of reptiles may confer some resilience to fire, survival is shaped by the availability and effectiveness of refuges. Where, for example, burrows, termite mounds, rock crevices and unburned vegetation can provide immediate shelters for survival (Robinson et al., 2013; Rego et al., 2021).

The sensitivity of medium- and large-sized mammals to fire is species-specific (Souza et al., 2023). During the 2020 megafire in the Pantanal, individuals from 26 of the 27 medium- and large-sized mammal species present in the area perished, with an estimated average mortality of approximately 49,000 individuals (Brack et al., 2024). Among the most affected species, *Tayassu pecari*, *Dasyprocta azarae*, and *Tapirus terrestris* had the highest number of identified records in this study, and they were also among the nine species with the highest mortality estimates from the 2020 fire event in the Pantanal (Brack et al., 2024).

Burned areas one year after wildfires exhibit lower bird diversity and a species composition distinct than unburned areas, indicating that some groups are more susceptible to environmental changes than others, depending on their ecological traits and habitat preferences (Schuchmann et al., 2024). However, despite their high mobility and relatively large body size, there is evidence suggesting that fire events may drive a process of biotic simplification and homogenization within bird communities (Ribeiro et al., 2024; Ribeiro et al., 2025). Although the exact mechanisms remain unclear, factors such as the lack of nearby refuges and larger home range requirements are suspected to play a key role in understanding their vulnerability (Ribeiro et al., 2024).

4.3. Effects of Mammal Mortality on Ecosystem Services

Among the ES provided by mammals and analyzed in this study, the most affected include disease sentinels, cultural services of charismatic species, ecotourism, and seed dispersal (Figure 4). Disease sentinelling, for example, is a density-dependent process that, under conditions of imbalance, can increase the prevalence of infectious diseases in humans (Guterres & de Lemos, 2018). Wildlife often serves as early indicators of disease outbreaks, displaying initial signs of pathogens present in the environment (Ojeyinka & Omaghomi, 2024). Their absence hinders the early detection of these threats, compromising their role as essential biological indicators (Civitello et al., 2015; Lacher Jr. et al., 2019).

The loss of cultural services associated with charismatic species and ecotourism can result in significant economic losses. For instance, in 2015, ecotourism centered around jaguars generated an annual gross revenue of nearly USD 7 million in a relatively small area (81,000 ha) of the Brazilian Pantanal wetlands (Tortato et al., 2017). This amount was three times higher than the revenue derived from traditional cattle ranching (Bogoni et al., 2020).

The decline of seed-dispersing animals has direct negative effects on plant regeneration (Landim et al., 2022), potentially leading to functional homogenization, which reduces the diversity of interactions and makes ecosystems less resilient to changes and disturbances (Mittelman et al., 2021). Moreover, defaunation of large frugivores in tropical forests can reduce carbon sequestration, affecting voluntary carbon markets (Bello et al., 2021). This loss not only compromises ecosystem functioning but also the benefits these systems provide to humanity (Santos et al., 2017). The impact of fire on seed dispersal raises significant concerns regarding ecosystem integrity (Harmange et al., 2024).

The transport of nutrients, related to the energy flux through trophic chains, can also be impacted by fire. Predator-prey interactions may be rapidly altered (Jorge et al., 2020). Prey species that depend on dense habitat structures face higher predation after fires, while others benefit from the opening of vegetation, which facilitates predator detection and escape (Doherty et al., 2022). Moreover, local defaunation can cause cascading effects within the community, where the absence of a species at one trophic level influences species at other levels, ultimately affecting ecosystem functioning (Landim et al., 2024).

Large and medium-sized mammal species are a fundamental part of trophic chains (Lacher Jr. et al., 2019), occupying different levels, where the disruption of links between levels, through the disappearance of small species, can reduce ecosystem resilience (Cassin & Matthews, 2021). An example is the jaguar (*Panthera onca*), the primary large predator in Brazil (Foster et al., 2013). In the Pantanal, fires caused injuries, displacement, hunger, dehydration and affected the species' abundance (de Barros et al., 2022; Bardales et al., 2024). These impacts can, consequently, affect prey availability and, therefore, the ecological stability of the region (de Barros et al., 2022).

Thus, like many mammals, reptiles, amphibians, and birds also play roles in nutrient transport, biological pest control, ecosystem engineering, pollination, and seed dispersal (Valencia-Aguilar et al., 2013; Cortéz-Gómez et al., 2015; Gaston, 2022; Schuchmann et al., 2024). Additionally, birds also provide regulation services through scavenging, performing a key role in mitigating greenhouse gases (Plaza & Lambertucci, 2022). They play a potential role in controlling agricultural pests, including weeds, insects, and rodents (by raptors) (Gaston, 2022). Furthermore, they are an important part of ecotourism services, through birdwatching (Byrd et al., 2024).

5. Conclusions and Future Directions

This study contributes to expanding knowledge about the direct effects of fire on wildlife in Brazil, providing valuable information to enhance conservation efforts. The results indicated that small vertebrates and reptiles are the groups most affected by fire. Among the ecosystem services impacted by mammal mortality, disease sentinelling, cultural service charismatic species, ecotourism and seed dispersal stands out as the most affected due to the high number of individuals associated with this function. It is also important to note that, in addition to the ecosystem services and ecological functions provided by these animals, they also play a significant role in mitigating and adapting to climate change (Pörtner et al., 2023; Pereira et al., 2024).

Based on these findings, we recommend: i) promote engagement of the scientific community and investment in repositories and databases, adopting standardized protocols for data collection, storage, and sharing; ii) implement prescribed burns to prevent uncontrolled fires and preserve vegetation mosaics, with fire sensitive and fire prone environmental, and their biodiversity, threatened by homogenization resulting from altered fire regimes; iii) conduct research focused on spatial analysis of potential refuges or fire islands, which play a crucial role in recolonizing areas previously impacted by fire; iv) apply genetic methodologies to analyze survival, characterize population genetic structure, and monitor biodiversity; and v) implement participatory public policies involving all stakeholders and fire-use interests, focusing on the integration of social sustainability with environmental conservation, as well as proper land-use planning, optimized agricultural practices, and fire protection. These recommendations reinforce the urgency of effective actions to mitigate fire damage and contribute to maintaining ecosystem integrity.

CRediT authorship contribution statement

Alessandra Rezende Pereira: Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Writing – review & editing. Fillipe Tamiozzo Pereira Torres: Writing – review & editing, Supervision, Resources, Conceptualization. Christian Niel Berlinck: Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors acknowledge the financial support provided by the Coordination for the Improvement of Higher Education Personnel (CAPES - financing code 001) and National Council for Scientific and logical Development (CNPq) for the scholarship granted to A. R. Pereira (this article is a part of her Master's research). We would also like to thank the ONG Onçafari, which kindly provided its field data, and all those who gathered and recorded field data and kindly provided us with the images. We would also like to thank the firefighters, managers and people directly involved in firefighting and carrying out the prescribed burning. Finally, we would like to thank the identification experts for their collaboration in identifying many animals. CNB thanks ICMBio and CNPq/MCTI/FNDCT (nº 18/2021, process nº 406473/2021-8) for field support.

Data availability

The database is available at: Pereira, A. R., Torres, F. T. P., Berlinck, C. N., 2025. Direct Impacts of Fire on Vertebrates [dataset]. Mendeley Data, V1.

https://doi.org/10.17632/hpd9mwpc6h.1

References

Alencar, A. A., Brando, P. M., Asner, G. P., & Putz, F. E. (2015). Landscape fragmentation, severe drought, and the new Amazon forest fire regime. *Ecological Applications*, 25(6), 1493-1505. https://doi.org/10.1890/14-1528.1

Anjos, A. G., Alvarado, S. T., Solé, M., & Benchimol, M. (2024). Influence of fire regime on the taxonomic and phylogenetic diversity of frog communities in a fire-prone Brazilian ecosystem. *Forest Ecology and Management*, 551, 121556. https://doi.org/10.1016/j.foreco.2023.121556

Atkins, Z., Clemann, N., & Robert, K. A. (2015). Does shelter site selection aid persistence of a threatened alpine lizard? Assessing Liopholis guthega populations a decade after severe fire in southeastern Australia. *Journal of Herpetology*, *49*(2), 222-229. https://doi.org/10.1670/13-194

August, T., Powney, G., Harrower, C., Hill, M., & Isaac, N. (2015). sparta: Trend Analysis for Unstructured Data. R package version 0.1. 30.

Batista, E. K., Figueira, J. E., Solar, R. R., de Azevedo, C. S., Beirão, M. V., Berlinck, C. N., ... & Fernandes, G. W. (2023). In case of fire, escape or die: a trait-based approach for identifying animal species threatened by fire. *Fire*, 6(6), 242. https://doi.org/10.3390/fire6060242

Bardales, R., Boron, V., Passos Viana, D. F., Sousa, L. L., Dröge, E., Porfirio, G., ... & Hyde, M. (2024). Neotropical mammal responses to megafires in the Brazilian Pantanal. *Global Change Biology*, 30(4), e17278. https://doi.org/10.1111/gcb.17278

Barlow, J. & Silveira, J. M. (2009). The consequences of fire for the fauna of humid tropical forests. In: Cochrane, M. A. (Eds.), *Tropical fire ecology: climate change, land use, and ecosystem dynamics*, (pp. 543-556). Springer, Berlin. https://doi.org/10.1007/978-3-540-77381-8_19

Bello, C., Culot, L., Agudelo, C. A. R., & Galetti, M. (2021). Valuing the economic impacts of seed dispersal loss on voluntary carbon markets. *Ecosystem Services*, 52, 101362. https://doi.org/10.1016/j.ecoser.2021.101362

Bergstrom, B. J., Scruggs, S. B., & Vieira, E. M. (2023). Tropical savanna small mammals respond to loss of cover following disturbance: A global review of field studies. *Frontiers in Ecology and Evolution*, 11, 1017361. https://doi.org/10.3389/fevo.2023.1017361

Berlinck, C. N., Lima, L. H. A., & Carvalho Junior, E. A. R. D. (2021). Historical survey of research related to fire management and fauna conservation in the world and in Brazil. *Biota Neotropica*, 21, e20201144. https://doi.org/10.1590/1676-0611-BN-2020-1144

Bícego, K. C. (2020). Ectotermia e endotermia. In: *Fisiologia Térmica de Vertebrados* (pp. 69-87). São Paulo: Cultura Acadêmica. ISBN: 978-85-7249-066-5.

Bogoni, J. A., Peres, C. A., & Ferraz, K. M. (2020). Effects of mammal defaunation on natural ecosystem services and human well being throughout the entire Neotropical realm. *Ecosystem Services*, 45, 101173. https://doi.org/10.1016/j.ecoser.2020.101173

Bonney, R. (2021). Expanding the impact of citizen science. *BioScience*, 71(5), 448-451. https://doi.org/10.1093/biosci/biab041

Bowman, D. M., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., ... & Pyne, S. J. (2009). Fire in the Earth system. *Science*, 324(5926), 481-484. https://doi.org/10.1126/science.1163886

Bowman, D. M., Kolden, C. A., Abatzoglou, J. T., Johnston, F. H., van der Werf, G. R., & Flannigan, M. (2020). Vegetation fires in the Anthropocene. *Nature Reviews Earth & Environment*, 1(10), 500-515. https://doi.org/10.1038/s43017-020-0085-3

Brack, I. V., Cordeiro, J. L., Kindel, A., Rangel, B. Z., Crawshaw, D., Heiermann, D., ... & de Oliveira, L. F. (2024). Spatial modelling and estimation of mammals' mortalities by Pantanal 2020 megafires. *Journal of Applied Ecology*, 61(11), 2848-2859. https://doi.org/10.1111/1365-2664.14789

Brown Jr., K. S. (1986). Zoogeografia da região do Pantanal Mato-grossense. In: Anais do Simpósio sobre Recursos Naturais e Sócio-Econômicos do Pantanal, Brasília, DF: EMBRAPA (pp. 137-179).

Byrd, K. B., Woo, I., Hall, L., Pindilli, E., Moritsch, M., Good, A., ... & Nakai, G. (2024). Birdwatching preferences reveal synergies and tradeoffs among recreation, carbon, and fisheries ecosystem services in Pacific Northwest estuaries, USA. *Ecosystem Services*, 69, 101656. https://doi.org/10.1016/j.ecoser.2024.101656

Callaghan, C. T., Winnebald, C., Smith, B., Mason, B. M., & López-Hoffman, L. (2024). Citizen science as a valuable tool for environmental review. *Frontiers in Ecology and the Environment*, e2808. https://doi.org/10.1002/fee.2808

Cassin, J., & Matthews, J. H. (2021). Nature-based solutions, water security and climate change: Issues and opportunities. In: *Nature-Based Solutions and Water Security* (pp. 63-79). Elsevier. https://doi.org/10.1016/B978-0-12-819871-1.00017-8

Chandler, M., See, L., Copas, K., Bonde, A. M., López, B. C., Danielsen, F., ... & Turak, E. (2017). Contribution of citizen science towards international biodiversity monitoring. *Biological Conservation*, 213, 280-294. https://doi.org/10.1016/j.biocon.2016.09.004

Chiarello, A. G. (2000). Density and population size of mammals in remnants of Brazilian Atlantic Forest. *Conservation Biology*, 14(6), 1649-1657. https://doi.org/10.1111/j.1523-1739.2000.99071.x

Civitello, D. J., Cohen, J., Fatima, H., Halstead, N. T., Liriano, J., McMahon, T. A., ... & Rohr, J. R. (2015). Biodiversity inhibits parasites: broad evidence for the dilution effect. *Proceedings of the National Academy of Sciences*, 112(28), 8667-8671. https://doi.org/10.1073/pnas.1506279112

Cortéz-Gómez, A. M. M., Ruiz-Agudelo, C. A., Valencia-Aguilar, A., & Ladle, R. J. (2015). Ecological functions of neotropical amphibians and reptiles: a review. *Universitas Scientiarum*, 20(2), 229-245. https://doi.org/10.11144/Javeriana.SC20-2.efna

Costa, A. G, Torres, F. T. P., Lima, G. S., Melo, F. R., Rodrigues, V. B., Santana Neto, V. P., Fernandes, T. V. (2022). Fire Influence on the Ants Community in Savanic and Forest Environments of the Cerrado Biome; *Floram*, 29(1), e20220025. https://doi.org/10.1590/2179-8087-FLORAM-2022-0025

Costa, B. M., Pantoja, D. L., Vianna, M. C. M., & Colli, G. R. (2013). Direct and short-term effects of fire on lizard assemblages from a Neotropical savanna hotspot. *Journal of Herpetology*, *47*(3), 502-510. https://doi.org/10.1670/12-043

Couto, E. G., Corrêa, G. R., Oliveira, V. A., do Nascimento, A. F., Vidal-Torrado, P., Beirigo, R., & Schaefer, C. E. G. R. (2023). Soils of Pantanal: the largest continental wetland. In: *The Soils of Brazil* (pp. 239–267). Springer International Publishing. https://doi.org/10.1007/978-3-031-19949-3_9

Damasceno-Junior, G.A., Pereira, A.d.M.M., Oldeland, J., Parolin, P., Pott, A. (2021). Fire, Flood and Pantanal Vegetation. In: Damasceno-Junior, G.A., Pott, A. (Eds.), *Flora and Vegetation of the Pantanal Wetland*. Plant and Vegetation (pp. 661–688). Springer International Publishing. https://doi.org/10.1007/978-3-030-83375-6_18

de Andrade, C. F., Delgado, R. C., Barbosa, M. L. F., Teodoro, P. E., da Silva Junior, C. A., Wanderley, H. S., & Capristo-Silva, G. F. (2020). Fire regime in Southern Brazil driven by atmospheric variation and vegetation cover. *Agricultural and Forest Meteorology*, 295, 108194. https://doi.org/10.1016/j.agrformet.2020.108194

de Barros, A. E., Morato, R. G., Fleming, C. H., Pardini, R., Oliveira-Santos, L. G. R., Tomas, W. M., ... & Prado, P. I. (2022). Wildfires disproportionately affected jaguars in the Pantanal. *Communications Biology*, 5(1), 1028. https://doi.org/10.1038/s42003-022-03937-1

de França Gomes, B. (2024). Efeitos diretos e indiretos do fogo sobre pequenos vertebrados de áreas campestres. Tese (Doutorado). Instituto de Biociências da Universidade de São Paulo, 165 p.

Doherty, T. S., Geary, W. L., Jolly, C. J., Macdonald, K. J., Miritis, V., Watchorn, D. J., ... & Dickman, C. R. (2022). Fire as a driver and mediator of predator–prey interactions. *Biological Reviews*, 97(4), 1539-1558. https://doi.org/10.1111/brv.12853

dos Santos Ferreira, B. H., da Rosa Oliveira, M., Fernandes, R. A. M., Nacagava, V. A. F., Arguelho, B. A., Ribeiro, D. B., ... & Garcia, L. C. (2023). Flowering and fruiting show phenological complementarity in both trees and non-trees in mosaic-burnt floodable savanna. *Journal of Environmental Management*, 337, 117665. https://doi.org/10.1016/j.jenvman.2023.117665

Duane, A., Castellnou, M., & Brotons, L. (2021). Towards a comprehensive look at global drivers of novel extreme wildfire events. *Climatic Change*, 165(3), 43. https://doi.org/10.1007/s10584-021-03066-4

Durigan, G., Pilon, N. A., Abreu, R. C., Hoffmann, W. A., Martins, M., Fiorillo, B. F., ... & Vasconcelos, H. L. (2020). No net loss of species diversity after prescribed fires in the Brazilian savanna. *Frontiers in Forests and Global Change*, 3, 13. https://doi.org/10.3389/ffgc.2020.00013

Dyer, R. J., Gillings, S., Pywell, R. F., Fox, R., Roy, D. B., & Oliver, T. H. (2017). Developing a biodiversity-based indicator for large-scale environmental assessment: a case study of proposed shale gas extraction sites in Britain. *Journal of Applied Ecology*, 54(3), 872-882. https://doi.org/10.1111/1365-2664.12784

Emmons, L. H. & Feer, F. (1997). Neotropical Rainforest Mammals: A Field Guide. University of Chicago Press, Chicago and London.

Engstrom, R. T. (2010). First-order fire effects on animals: review and recommendations. *Fire Ecology*, 6, 115-130. https://doi.org/10.4996/fireecology.0601115

Ensbey, M., Legge, S., Jolly, C. J., Garnett, S. T., Gallagher, R. V., Lintermans, M., ... & Zukowski, S. (2023). Animal population decline and recovery after severe fire: Relating ecological and life history traits with expert estimates of population impacts from the Australian 2019-20 megafires. *Biological Conservation*, 283, 110021. https://doi.org/10.1016/j.biocon.2023.110021

Feng, X., Merow, C., Liu, Z., Park, D. S., Roehrdanz, P. R., Maitner, B., ... & Enquist, B. J. (2021). How deregulation, drought and increasing fire impact Amazonian biodiversity. *Nature*, 597(7877). https://doi.org/10.1038/s41586-021-03876-7

Fonseca, M. G., Anderson, L. O., Arai, E., Shimabukuro, Y. E., Xaud, H. A., Xaud, M. R., ... & Aragão, L. E. (2017). Climatic and anthropogenic drivers of northern Amazon fires during the 2015–2016 El Niño event. *Ecological Applications*, 27(8), 2514-2527. https://doi.org/10.1002/eap.1628

Foster, V. C., Sarmento, P., Sollmann, R., Tôrres, N., Jácomo, A. T., Negrões, N., ... & Silveira, L. (2013). Jaguar and puma activity patterns and predator-prey interactions in four Brazilian biomes. *Biotropica*, 45(3), 373-379. https://doi.org/10.1111/btp.12021

Fullagar, H. H., Schwarz, E., Richardson, A., Notley, S. R., Lu, D., & Duffield, R. (2021). Australian firefighters perceptions of heat stress, fatigue and recovery practices during fire-fighting tasks in extreme environments. *Applied Ergonomics*, 95, 103449. https://doi.org/10.1016/j.apergo.2021.103449

Garcia, L. C., Szabo, J. K., de Oliveira Roque, F., Pereira, A. D. M. M., da Cunha, C. N., Damasceno-Júnior, G. A., ... & Ribeiro, D. B. (2021). Record-breaking wildfires in the world's largest continuous tropical wetland: Integrative fire management is urgently needed for both biodiversity and humans. *Journal of Environmental Management*, 293, 112870. https://doi.org/10.1016/j.jenvman.2021.112870

Gaston, K. J. (2022). Birds and ecosystem services. *Current Biology*, 32(20), R1163-R1166. https://doi.org/10.1016/j.cub.2022.07.053

Giorgis, M. A., Zeballos, S. R., Carbone, L., Zimmermann, H., von Wehrden, H., Aguilar, R., ... & Jaureguiberry, P. (2021). A review of fire effects across South American ecosystems: the role of climate and time since fire. *Fire Ecology*, 17, 1-20. https://doi.org/10.1186/s42408-021-00100-9

González, T. M., González-Trujillo, J. D., Muñoz, A., & Armenteras, D. (2021). Differential effects of fire on the occupancy of small mammals in neotropical savanna-gallery forests. *Perspectives in Ecology and Conservation*, 19(2), 179-188. https://doi.org/10.1016/j.pecon.2021.03.005

González, T. M., González-Trujillo, J. D., Muñoz, A., & Armenteras, D. (2022). Effects of fire history on animal communities: a systematic review. *Ecological Processes*, 11(1), 1-11. https://doi.org/10.1186/s13717-021-00357-7

González-Fernández, A., Couturier, S., Dotor-Diego, R., Martínez-Díaz-González, R., & Sunny, A. (2024). Direct fire-induced reptile mortality in the Sierra Morelos natural protected area (Mexico). *Herpetozoa*, *37*, 213. https://doi.org/10.3897/herpetozoa.37.e116376

Gorissen, S., Greenlees, M., & Shine, R. (2018). The impact of wildfire on an endangered reptile (*Eulamprus leuraensis*) in Australian montane swamps. *International Journal of Wildland Fire*, *27*(7), 447-456. https://doi.org/10.1071/WF17048

Griffiths, A. D., & Brook, B. W. (2014). Effect of fire on small mammals: a systematic review. *International Journal of Wildland Fire*, 23(7), 1034-1043. https://doi.org/10.1071/WF14026

Guillera-Arroita, G. (2017). Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. *Ecography*, 40(2), 281-295. https://doi.org/10.1111/ecog.02445

Guimarães, A. F., Querido, L. C. A., Rocha, T., Rodrigues, D. J., Viana, P. L., Bergallo, H. G., ... & Dala-Corte, R. B. (2024). Disentangling the veil line for Brazilian biodiversity: An overview from two long-term research programs reveals huge gaps in ecological data reporting. *Science of The Total Environment*, 174880. https://doi.org/10.1016/j.scitotenv.2024.174880

Guterres, A., & de Lemos, E. R. S. (2018). Hantaviruses and a neglected environmental determinant. *One Health*, 5, 27-33. https://doi.org/10.1016/j.onehlt.2017.12.002

Harmange, C., Teles, T. S., Ribeiro, D. B., Costa, A. M., Godoi, M. N., de Oliveira Roque, F., ... & Pays, O. (2024). Fire shapes mammal abundance at the Cerrado-Pantanal ecotone: Scale of effect, species traits and land cover interaction. *Journal for Nature Conservation*, 126728. https://doi.org/10.1016/j.jnc.2024.126728

Hill, M. O. (2012). Local frequency as a key to interpreting species occurrence data when recording effort is not known. *Methods in Ecology and Evolution*, 3(1), 195-205. https://doi.org/10.1111/j.2041-210X.2011.00146.x

Isaac, N. J., van Strien, A. J., August, T. A., de Zeeuw, M. P., & Roy, D. B. (2014). Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution*, 5(10), 1052-1060. https://doi.org/10.1111/2041-210X.12254

Jacobs, I. (2022). Animal response to fire. In: Vonk, J., Shackelford, T.K. (eds). *Encyclopedia of animal cognition and behavior* (pp. 314-317). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-55065-7_2095

Jacobs, I., von Bayern, A. M., & Osvath, M. (2021). Tools and food on heat lamps: pyrocognitive sparks in New Caledonian crows?. *Behaviour*, *159*(6), 591-602. https://doi.org/10.1163/1568539X-bja10138

Jeklin, A. T., Davies, H. W., Bredin, S. S., Hives, B. A., Meanwell, L. E., Perrotta, A. S., & Warburton, D. E. (2020). Fatigue and sleep patterns among Canadian wildland firefighters during a 17-day fire line deployment. *Journal of Occupational and Environmental Hygiene*, 17(7-8), 364-371. https://doi.org/10.1080/15459624.2020.1759809

Johnston, A., Hochachka, W., Strimas-Mackey, M., Gutierrez, V. R., Robinson, O., Miller, E., ... & Fink, D. (2019). Analytical guidelines to increase the value of citizen science data: using eBird data to estimate species occurrence. *BioRxiv*, 574392. https://doi.org/10.1101/574392

Jolly, C. J., Dickman, C. R., Doherty, T. S., van Eeden, L. M., Geary, W. L., Legge, S. M., ... & Nimmo, D. G. (2022). Animal mortality during fire. *Global Change Biology*, 28(6), 2053-2065. https://doi.org/10.1111/gcb.16044

Jordaan, P. R., Steyl, J. C., Hanekom, C. C., & Combrink, X. (2020). Fire-associated reptile mortality in Tembe Elephant Park, South Africa. *Fire Ecology*, 16, 1-6. https://doi.org/10.1186/s42408-019-0066-4

Jorge, M. H., Garrison, E. P., Conner, L. M., & Cherry, M. J. (2020). Fire and land cover drive predator abundances in a pyric landscape. *Forest Ecology and Management*, 461, 117939. https://doi.org/10.1016/j.foreco.2020.117939

Kamp, J., Oppel, S., Heldbjerg, H., Nyegaard, T., & Donald, P. F. (2016). Unstructured citizen science data fail to detect long-term population declines of common birds in Denmark. *Diversity and Distributions*, 22(10), 1024–1035. https://doi.org/10.1111/ddi.12463

Kelly, L. T., Giljohann, K. M., Duane, A., Aquilué, N., Archibald, S., Batllori, E., ... & Brotons, L. (2020). Fire and biodiversity in the Anthropocene. *Science*, 370(6519), eabb0355. https://doi.org/10.1126/science.abb03

Kosmala, M., Wiggins, A., Swanson, A., & Simmons, B. (2016). Assessing data quality in citizen science. *Frontiers in Ecology and the Environment*, 14(10), 551-560. https://doi.org/10.1002/fee.1436

Lacet, C., Olifiers, N., & Bueno, C. (2023). Immediate impact of fires on roadkilling of wild vertebrates on a highway in southeast Brazil. *Perspectives in Ecology and Conservation*, 21(3), 231-236. https://doi.org/10.1016/j.pecon.2023.07.002

Lacher Jr., T. E., Davidson, A. D., Fleming, T. H., Gómez-Ruiz, E. P., McCracken, G. F., Owen-Smith, N., ... & Vander Wall, S. B. (2019). The functional roles of mammals in ecosystems. *Journal of Mammalogy*, 100(3), 942-964. https://doi.org/10.1093/jmammal/gyy183

Landim, A. R., Fernandez, F. A., & Pires, A. (2022). Primate reintroduction promotes the recruitment of large-seeded plants via secondary dispersal. *Biological Conservation*, 269, 109549. https://doi.org/10.1016/j.biocon.2022.109549

Landim, A. R., Guimarães Jr., P. R., Fernandez, F. A., & Dias, A. T. C. (2024). A framework for the restoration of seed dispersal and pollination. *Restoration Ecology*, e14151. https://doi.org/10.1111/rec.14151

Lewis, D. (2020). 'Deathly silent': Ecologist describes Australian wildfires' devastating aftermath. *Nature*, 577(7790):304-304. https://doi.org/10.1038/D41586-020-00043-2

Libonati, R., DaCamara, C. C., Peres, L. F., Sander de Carvalho, L. A., & Garcia, L. C. (2020). Rescue Brazil's burning Pantanal wetlands. *Nature*, 588(7837), 217-219. https://doi.org/10.1038/d41586-020-03464-1

Lindenmayer, D. B., Kooyman, R. M., Taylor, C., Ward, M., & Watson, J. E. (2020). Recent Australian wildfires made worse by logging and associated forest management. *Nature Ecology & Evolution*, 4(7), 898-900. https://doi.org/10.1038/s41559-020-1195-5

Linley, G. D., Geary, W. L., Jolly, C. J., Spencer, E. E., Ashman, K. R., Michael, D. R., ... & Nimmo, D. G. (2024). Wombat burrows are hotspots for small vertebrates in a landscape subject to gigafire. *Journal of Mammalogy*, gyae034. https://doi.org/10.1093/jmammal/gyae034

Magioli, M., Lima, L. H. A., Villela, P. M. S., Sampaio, R., Bonjorne, L., Ribeiro, R. L. A., ... & Berlinck, C. N. (2024). Forest type modulates mammalian responses to megafires. *Scientific Reports*, 14(1), 13538. https://doi.org/10.1038/s41598-024-64460-3

Mahony, M., Gould, J., Beranek, C. T., Callen, A., Clulow, J., Clulow, S., ... & Pickett, E. (2022). A trait-based analysis for predicting impact of wildfires on frogs. *Australian Zoologist*, 42(2), 326-351. https://doi.org/10.7882/AZ.2022.021

Mandeville, C. P., Nilsen, E. B., Herfindal, I., & Finstad, A. G. (2023). Participatory monitoring drives biodiversity knowledge in global protected areas. *Communications Earth & Environment*, 4(1), 240. https://doi.org/10.1038/s43247-023-00906-2

Martins, P. I., Belém, L. B. C., Szabo, J. K., Libonati, R., & Garcia, L. C. (2022). Prioritising areas for wildfire prevention and post-fire restoration in the Brazilian Pantanal. *Ecological Engineering*, 176, 106517. https://doi.org/10.1016/j.ecoleng.2021.106517

McLauchlan, K. K., Higuera, P. E., Miesel, J., Rogers, B. M., Schweitzer, J., Shuman, J. K., ... & Watts, A. C. (2020). Fire as a fundamental ecological process: Research advances and frontiers. *Journal of Ecology*, 108(5), 2047-2069. https://doi.org/10.1111/1365-2745.13403

McWethy, D. B., Schoennagel, T., Higuera, P. E., Krawchuk, M., Harvey, B. J., Metcalf, E. C., ... & Kolden, C. (2019). Rethinking resilience to wildfire. *Nature Sustainability*, 2(9), 797-804. https://doi.org/10.1038/s41893-019-0353-8

Mendonça, A. F., Armond, T., Camargo, A. C. L., Camargo, N. F., Ribeiro, J. F., Zangrandi, P. L., & Vieira, E. M. (2015). Effects of an extensive fire on arboreal small mammal populations in a neotropical savanna woodland. *Journal of Mammalogy*, 96(2), 368-379. https://doi.org/10.1093/jmammal/gyv038

Michel, A., Johnson, J. R., Szeligowski, R., Ritchie, E. G., & Sih, A., 2023. Integrating sensory ecology and predator-prey theory to understand animal responses to fire. *Ecology Letters*, 26(7), 1050-1070. https://doi.org/10.1111/ele.14231

Mittelman, P., Landim, A. R., Genes, L., Assis, A. P. A., Starling-Manne, C., Leonardo, P. V., ... & Pires, A. S. (2022). Trophic rewilding benefits a tropical community through direct and indirect network effects. *Ecography*, 4. https://doi.org/10.1111/ecog.05838

Moritz, M. A., Batllori, E., & Bolker, B. M. (2023). The role of fire in terrestrial vertebrate richness patterns. *Ecology Letters*, 26(4), 563-574. https://doi.org/10.1111/ele.14177

Nieman, W. A., van Wilgen, B. W., Radloff, F. G., & Leslie, A. J. (2021). A review of the responses of medium-to large-sized African mammals to fire. *African Journal of Range & Forage Science*, 39(3), 249-263. https://doi.org/10.2989/10220119.2021.1918765

Nimmo, D. G., Avitabile, S., Banks, S. C., Bliege Bird, R., Callister, K., Clarke, M. F., ... & Bennett, A. F. (2019). Animal movements in fire-prone landscapes. *Biological Reviews*, 94(3), 981-998. https://doi.org/10.1111/brv.12486

Nimmo, D. G., Carthey, A. J. R., Jolly, C. J., & Blumstein, D. T. (2021). Welcome to the Pyrocene: Animal survival in the age of megafire. *Global Change Biology*, 27(22), 5684–5693. https://doi.org/10.1111/gcb.15834

O, S., Hou, X. & Orth, R. (2020). Observational evidence of wildfire-promoting soil moisture anomalies. *Scientific Reports*, 10(1), 1-8. https://doi.org/10.1038/s41598-020-67530-4

Ojeyinka, O. T., & Omaghomi, T. T. (2024). Wildlife as sentinels for emerging zoonotic diseases: A review of surveillance systems in the USA. *World Journal of Advanced Research and Reviews*, 21(3), 768-778. https://doi.org/10.30574/wjarr.2024.21.3.0773

Oliver, T. H., Heard, M. S., Isaac, N. J., Roy, D. B., Procter, D., Eigenbrod, F., ... & Bullock, J. M. (2015). Biodiversity and resilience of ecosystem functions. *Trends in Ecology & Evolution*, 30(11), 673-684. https://doi.org/10.1016/j.tree.2015.08.009

Oliveira, J. C., Castro, T. M., Silva-Soares, T., & Rocha, C. F. D. (2019). First-order effects of fire and prolonged-drought effects on an undescribed semi-aquatic turtle in Atlantic rainforest in southeastern Brazil. *Journal of Coastal Conservation*, 23, 367-372. https://doi.org/10.1007/s11852-018-0668-z

Oliveira, U., Soares-Filho, B., Rodrigues, H., Figueira, D., Gomes, L., Leles, W., ... & Miranda, H. (2023). A near real-time web-system for predicting fire spread across the Cerrado biome. *Scientific Reports*, 13(1), 4829. https://doi.org/10.1038/s41598-023-30560-9

Pacheco, L. F., Quispe-Calle, L. C., Suárez-Guzmán, F. A., Ocampo, M., & Claure-Herrera, Á. J. (2021). Muerte de mamíferos por los incendios de 2019 en la Chiquitania. *Ecología en Bolivia: Revista del Instituto de Ecología*, 56(1), 4-16.

Paemelaere, E. A., Hallett, M. T., de Freitas, K., Balvadore, S., Ignace, M., Mandook, A., ... & van Vliet, N. (2024). Medium and large mammal responses to fire in a neotropical savanna system in Guyana. *Biotropica*, e13397. https://doi.org/10.1111/btp.13397

Pausas, J. G. (2019). Generalized fire response strategies in plants and animals. *Oikos*, 128(2), 147-153. https://doi.org/10.1111/oik.05907

Pausas, J. G., & Parr, C. L. (2018). Towards an understanding of the evolutionary role of fire in animals. *Evolutionary Ecology*, 32(2), 113-125. https://doi.org/10.1007/s10682-018-9927-6

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., ... & Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, 355(6332), eaai9214. https://doi.org/10.1126/science.aai9214

Pelissari, T. D., Teodoro, P. E., Teodoro, L. P. R., Lima, M., Santana, D. C., Rossi, F. S., ... & da Silva Junior, C. A. (2023). Dynamics of major environmental disasters involving fire in the Brazilian Pantanal. *Scientific Reports*, 13(1), 21669. https://doi.org/10.1038/s41598-023-49154-6

Pereira, A. D. M. M., Oliveira, M. D. R., Bao, F., Souza, E. B. D., Pott, A., Escobar, A. C. D. S., ... & Damasceno-Júnior, G. A. (2024). Changes, trends, and gaps in research dynamics after the megafires in the Pantanal. *Environment, Development and Sustainability*, 1-15. https://doi.org/10.1007/s10668-024-05081-8

Pereira, C. C., Kenedy-Siqueira, W., Negreiros, D., Fernandes, S., Barbosa, M., Goulart, F. F., ... & Fernandes, G. W. (2024). Scientists' warning: six key points where biodiversity can improve climate change mitigation. *BioScience*, 74(5), 315-318. https://doi.org/10.1093/biosci/biae035

Pescott, O. L., Stroh, P. A., Humphrey, T. A., & Walker, K. J. (2022). Simple methods for improving the communication of uncertainty in species' temporal trends. *Ecological Indicators*, 141, 109117. https://doi.org/10.1016/j.ecolind.2022.109117

Pivello, V. R., Vieira, I., Christianini, A. V., Ribeiro, D. B., da Silva Menezes, L., Berlinck, C. N., ... & Overbeck, G. E. (2021). Understanding Brazil's catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. *Perspectives in Ecology and Conservation*, 19(3), 233-255. https://doi.org/10.1016/j.pecon.2021.06.005

Plaza, P. I., & Lambertucci, S. A. (2022). Mitigating GHG emissions: A global ecosystem service provided by obligate scavenging birds. *Ecosystem Services*, 56, 101455. https://doi.org/10.1016/j.ecoser.2022.101455

Pocknee, C. A., Legge, S. M., McDonald, J., & Fisher, D. O. (2023). Modeling mammal response to fire based on species' traits. *Conservation Biology*, 37(4), e14062. https://doi.org/10.1111/cobi.14062

Pörtner, H. O., Scholes, R. J., Arneth, A., Barnes, D. K. A., Burrows, M. T., Diamond, S. E., ... & Val, A. L. (2023). Overcoming the coupled climate and biodiversity crises and their societal impacts. *Science*, 380(6642), eabl4881. https://doi.org/10.1126/science.abl4881

R Core Team (2024). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rego, F. C., Morgan, P., Fernandes, P., Hoffman, C., Castro Rego, F., Morgan, P., ... & Hoffman, C. (2021). Fire effects on plants, soils, and animals. *Fire science: From chemistry to landscape management*, 259-318. https://doi.org/10.1007/978-3-030-69815-7_9

Ribeiro, A. C. D. C., Ortega, J. C., Bini, L. M., Ferro, V. G., Bispo, A. A., Carvalho, W. F., ... & Cianciaruso, M. V. (2025). The effect of fire on the structure of animal metacommunities in a Cerrado landscape: A 10-year survey of anurans, birds and moth assemblages. *Journal for Nature Conservation*, 126856. https://doi.org/10.1016/j.jnc.2025.126856

Ribeiro, A. C. D. C., Ortega, J. C., Bini, L. M., Ferro, V. G., Bispo, A. A., Carvalho, W. F., ... & Cianciaruso, M. V. (2024). The Effect of Catastrophic Fire on the Structure of Animal Metacommunities in a Cerrado Landscape: A 10-Year Survey of Anurans, Birds and Moth Assemblages. *Birds and Moth Assemblages*. http://doi.org/10.2139/ssrn.5023424

Ribeiro, A. F., Brando, P. M., Santos, L., Rattis, L., Hirschi, M., Hauser, M., ... & Zscheischler, J. (2022). A compound event-oriented framework to tropical fire risk assessment in a changing climate. *Environmental Research Letters*, 17(6), 065015. https://doi.org/10.1088/1748-9326/ac7342

Robinson, N. M., Leonard, S. W., Ritchie, E. G., Bassett, M., Chia, E. K., Buckingham, S., ... & Clarke, M. F. (2013). Refuges for fauna in fire-prone landscapes: their ecological function and importance. *Journal of Applied Ecology*, 50(6), 1321-1329. https://doi.org/10.1111/1365-2664.12153

Rodrigues, F. H. G., Medri, I. M., Tomas, W. M., & Mourão, G. M. (2002). Revisão do conhecimento sobre ocorrência e distribuição de mamíferos do Pantanal. EMBRAPA Pantanal, Corumbá. http://www.infoteca.cnptia.embrapa.br/infoteca/handle/doc/810726

Russell, K. R., Van Lear, D. H., & Guynn Jr, D. C. (1999). Prescribed fire effects on herpetofauna: review and management implications. *Wildlife Society Bulletin*, 27(2), 374–384.

Santos, G. C., Chaves, L. S., & Albuquerque, U. P. (2017). Loss of Seed-Dispersing Animals and Its Impacts on Humanity. *Ethnobiology and Conservation*, 6. https://doi.org/10.15451/ec2017-09-6.17-1-7

Santos, J. L., Hradsky, B. A., Keith, D. A., Rowe, K. C., Senior, K. L., Sitters, H., & Kelly, L. T. (2022). Beyond inappropriate fire regimes: A synthesis of fire-driven declines of threatened mammals in Australia. *Conservation Letters*, 15(5), e12905. https://doi.org/10.1111/conl.12905

Santos, J. L., Sitters, H., Keith, D. A., Geary, W. L., Tingley, R., & Kelly, L. T. (2022). A demographic framework for understanding fire-driven reptile declines in the 'land of the lizards'. *Global Ecology and Biogeography*, 31(10), 2105-2119. https://doi.org/10.1111/geb.13520

Schmidt, I. B., Moura, L. C., Ferreira, M. C., Eloy, L., Sampaio, A. B., Dias, P. A., & Berlinck, C. N. (2018). Fire management in the Brazilian savanna: First steps and the way forward. *Journal of Applied Ecology*, 55(5), 2094-2101. https://doi.org/10.1111/1365-2664.13118

Schuchmann, K. L., Burs, K., de Deus, F., Fieker, C. Z., Tissiani, A. S., & Marques, M. I. (2024). Bird Community Traits in Recently Burned and Unburned Parts of the Northeastern Pantanal, Brazil: A Preliminary Approach. *Sustainability*, 16(6), 2321. https://doi.org/10.3390/su16062321

Silveira, L., Henrique, F., Rodrigues, G., de Almeida Jácomo, A. T., & Diniz Filho, J. A. F. (1999). Impact of wildfires on the megafauna of Emas National Park, central Brazil. *Oryx*, 33(2), 108-114. https://doi.org/10.1046/j.1365-3008.1999.00039.x

Smith, A., Meulders, B., Bull, C. M., & Driscoll, D. (2012). Wildfire-induced mortality of Australian reptiles. *Herpetology Notes*, 5, 233-235.

Souza, C. V., Lourenço, Á., & Vieira, E. M. (2023). Species-specific responses of medium and large mammals to fire regime attributes in a fire-prone neotropical savanna. *Fire*, 6(3), 110. https://doi.org/10.3390/fire6030110

Stephens, S. L., Collins, B. M., Fettig, C. J., Finney, M. A., Hoffman, C. M., Knapp, E. E., ... & Wayman, R. B. (2018). Drought, tree mortality, and wildfire in forests adapted to frequent fire. *BioScience*, 68(2), 77-88. https://doi.org/10.1093/biosci/bix146

Stephens, S. L., Westerling, A. L., Hurteau, M. D., Peery, M. Z., Schultz, C. A., & Thompson, S. (2020). Fire and climate change: conserving seasonally dry forests is still possible. *Frontiers in Ecology and the Environment*, 18(6), 354-60. https://doi.org/10.1002/fee.2218

Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., ... & Edgar, G. J. (2013). Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature*, 501(7468), 539-542. https://doi.org/10.1038/nature12529

Swan, M., Christie, F., Sitters, H., York, A., & Di Stefano, J. (2015). Predicting faunal fire responses in heterogeneous landscapes: the role of habitat structure. *Ecological Applications*, 25(8), 2293-2305. https://doi.org/10.1890/14-1533.1C

Tomas, W. M., Berlinck, C. N., Chiaravalloti, R. M., Faggioni, G. P., Strüssmann, C., Libonati, R., ... & Morato, R. (2021). Distance sampling surveys reveal 17 million vertebrates directly killed by the 2020's wildfires in the Pantanal, Brazil. *Scientific Reports*, 11(1), 23547. https://doi.org/10.1038/s41598-021-02844-5

Tomas W. M., Cáceres N. C., Nunes A. P., Fischer E., Mourão G., Campos Z. (2010). Mammals in the Pantanal wetland, Brazil. In: Junk W. J., Da Silva C. J., Nunes da Cunha C., Wantzen K. M. (Eds.), *The Pantanal: Ecology, biodiversity and sustainable management of a large neotropical seasonal wetland* (pp. 563–595). Sofia-Moscow, Russia: Pensoft Publishers.

Tomas W. M., de Oliveira Roque F., Morato R. G., et al. (2019). Sustainability Agenda for the Pantanal Wetland: Perspectives on a Collaborative Interface for Science, Policy, and Decision-Making. *Tropical Conservation Science*, 12. https://doi.org/10.1177/1940082919872634

Tomassini, O., & Massolo, A. (2024). From fire to recovery: temporal-shift of predator–prey interactions among mammals in Mediterranean ecosystems. *Mammalian Biology*, 104(5), 583-600. https://doi.org/10.1007/s42991-024-00439-x

Torres, F. T. P., Lima, G. S., de Oliveira, E. R. S., Lourenço, L. F., Félix, F. R. F., & Ribeiro, G. A. (2020). Manual de Prevenção e Combate de Incêndios Florestais. Viçosa: UFV.

Tortato, F. R., Izzo, T. J., Hoogesteijn, R., & Peres, C. A. (2017). The numbers of the beast: Valuation of jaguar (Panthera onca) tourism and cattle depredation in the Brazilian Pantanal. *Global Ecology and Conservation*, 11, 106-114. https://doi.org/10.1016/j.gecco.2017.05.003

Tourinho, L., Manes, S., Pires, A. P., Nabout, J. C., Diniz-Filho, J. A. F., Terribile, L. C., ... & Vale, M. M. (2025). Projected impacts of climate change on ecosystem services provided by terrestrial mammals in Brazil. *Ecosystem Services*, 71, 101687. https://doi.org/10.1016/j.ecoser.2024.101687

Vale, M. M., Vieira, M. V., Grelle, C. E. V., Manes, S., Pires, A. P., Tardin, R. H., ... & Tourinho, L. (2023). Ecosystem services delivered by Brazilian mammals: spatial and taxonomic patterns and comprehensive list of species. *Perspectives in Ecology and Conservation*, 21(4), 302-310. https://doi.org/10.1016/j.pecon.2023.10.003

Valencia-Zuleta, A., Richter, A., do Valle Alvarenga, G., de Queiroz Batista, F. R., Moreira, L. F. B., Arbo-Meneses, B., ... & Côrtes, L. G. (2024). O fogo e a herpetofauna no Pantanal: observações durante e após os incêndios. *Biodiversidade Brasileira*, 14(4). https://doi.org/10.37002/biodiversidadebrasileira.v14i4.2556

Valencia-Aguilar, A., Cortés-Gómez, A. M., & Ruiz-Agudelo, C. A. (2013). Ecosystem services provided by amphibians and reptiles in Neotropical ecosystems. International *Journal of Biodiversity Science, Ecosystem Services & Management*, 9(3), 257-272. https://doi.org/10.1080/21513732.2013.821168

CHAPTER 2

Hidden Flames: Fire Survival, Ecological Traits, and Ecosystem Services of Brazilian Wildlife

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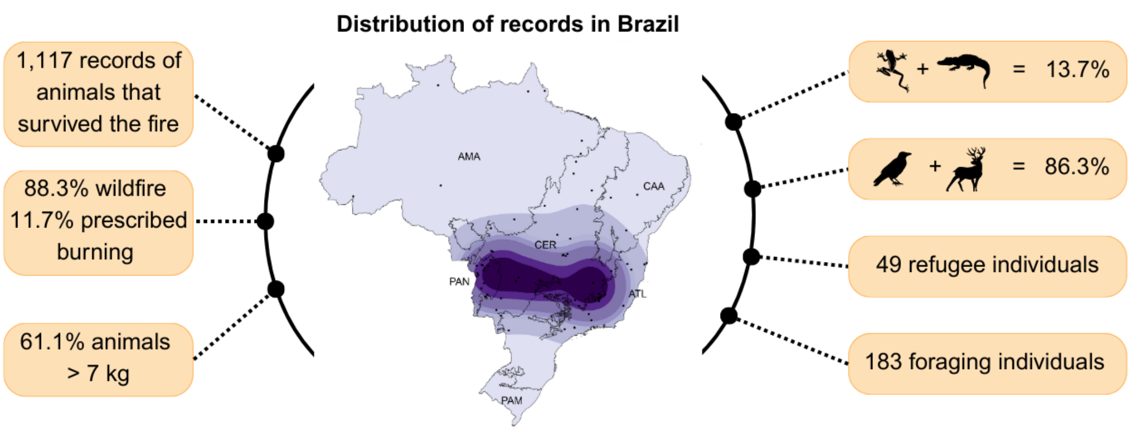
Manuscript submitted to the Journal *Acta Oecologica.*

Highlights:

- Vertebrates weighing more than 7 kg have the highest survival rates in fires in Brazil;
- Birds and mammals had the highest percentages of all records, at 14.7% and 71.6%, respectively;
- Amphibians and reptiles represented 0.9% and 12.8%, respectively;
- Reptiles were the group with the highest number of animals sheltered in burrows (59.1%);
- Ozotoceros bezoarticus and Rhea americana are the species with the highest probability of survival.

Graphical Abstract:



Abstract: Fire can affect animals both directly, through mortality and burns, and indirectly, through habitat alteration, the reduction of shelter and resources in surviving animals. Based on citizen science records, we evaluated animal survival in response to fire across Brazil. We compiled a database using images voluntarily submitted by firefighters, staff from environmental agencies, and researchers involved in fire suppression and prescribed burning activities. We recorded 1,117 animals indirectly impacted by fire, between 2006 and 2024, with 88.3% of the records related to wildfires and 11.7% to prescribed burns. These records were distributed among amphibians (0.9%), reptiles (12.8%), birds (14.7%), and mammals (71.6%). Regarding body size, 10.8% of the animals were classified as small, 28% as medium, and 61.1% as large. We identified 49 records of individuals sheltered in burrows and 183 showing opportunistic foraging behavior. We also found a higher likelihood of survival for the taxa Ozotoceros bezoarticus, Rhea americana, birds, Didelphidae, Myrmecophaga tridactyla, and Chelonoidis spp. Additionally, we recorded the ecosystem services provided by these groups, highlighting that R. americana, birds, and Didelphidae contribute to seed dispersal, a potentially essential service for the recolonization of burned areas.

Keywords: Fire regime; Wildfire; Prescribed burning; Fauna; Indirects effects; Second-order effects.

1. Introduction

Fire affects ecosystems worldwide, modifying habitats, altering resource availability, and consequently shaping the abundance and distribution of plants and animals (He et al., 2019; McLauchlan et al., 2020). In general, large wildfires can cause extensive animal mortality (see Tomas et al., 2021), characterizing the direct effects of fire, which also include injuries and burns (Engstrom, 2010; Batista et al., 2023). In fire-prone environments, animals have developed various fire-detection strategies to survive the direct impacts of fire, including chemoreception of smoke, heat sensitivity, visual perception of flames and smoke, and even auditory cues (Engstrom, 2010; Nowack et al., 2016; Mendyk et al., 2020; Jolly et al., 2022). Additionally, animals may adopt escape behaviors, fleeing to unburned refuges or seeking shelter in a safe place within the burned area, such as burrows (Nimmo et al., 2021). In this context, the morphology, behavior, and ecology of species significantly influence the impacts they experience (Pocknee et al., 2023; Ribeiro et al., 2025).

Indirect effects of fire mostly occur in the long and short term and mainly include habitat alteration (Engstrom, 2010; Rego et al., 2021). Thus, surviving the fire is not the only challenge animals face (Engstrom, 2010). After a wildfire, the reduction of shelter and resources, combined with increased exposure to predators, can increase risks for animals, affecting their survival and population dynamics (Doherty et al., 2022; Magioli et al., 2024). Post-fire survival and population recovery depend not only on in situ persistence but also on the availability and distribution of nearby refuges and the capacity for recolonization from unburned areas (Banks et al., 2011; Hale et al., 2021; Shaw et al., 2021). Surviving individuals often serve as founders for subsequent population recovery (Hale et al., 2021), and in some cases, exogenous recolonization or nucleated recovery from refuges can facilitate reestablishment (Banks et al., 2017). Therefore, the degree of environmental disturbance plays a crucial role in this process, as high-severity fires and megafires can eliminate potential refuges, severely limiting opportunities for survival and recolonization (Collins et al., 2019).

Despite the negative impacts mentioned, from a positive perspective, the diversity and abundance of some species may increase, particularly in fire-prone ecosystems (Moritz et al., 2023), depending on the fire regime and species' ecology (Magioli et al., 2024). Additionally, opportunistic species may benefit in certain cases, such as foraging, as fire makes resources available, including grass and leaf regrowth that serves as food for herbivores; fleeing prey or carcasses, which attract large predators and scavengers; and seeds released by heat or exposed in the soil, benefiting granivorous animals (Pausas & Parr, 2018).

Thus, any fire regime will have both species that benefit (“winners”) and those that are negatively affected (“losers”) (Andersen, 2021). It is worth noting that the adaptations of species from fire-prone environments are related to specific characteristics of the fire regime, such as frequency, intensity, severity, extent, and seasonality (Keeley et al., 2011; Pausas, 2018). These adaptations, however, are not uniformly distributed across ecosystems. In fire-adapted Brazilian biomes such as the Cerrado, Pampa, and Pantanal, many species may have evolved traits that enhance survival (Pivello et al., 2021). In contrast, in ecologically fire-sensitive biomes such as the Amazon and Atlantic Forest, fauna tend to lack such adaptations and are therefore more vulnerable to fire-related impacts (Pivello et al., 2021). This ecological variation highlights the need for biome-specific approaches when assessing the effects of fire on wildlife and developing conservation strategies.

Although research on fire and fauna has increased in recent years, substantial knowledge gaps remain regarding how fires affect many animal groups. Rigorous monitoring of wildlife population performance under disturbance or management interventions often depends on capturing and marking individuals (Foster et al., 2018). Several studies have assessed post-fire survival using capture–recapture methods (Pons et al., 2003; Lyet et al., 2009), or before-after-control-impact experimental using cameras trapp (Eriksson et al., 2025), or radiotracking (Garvey et al., 2008), while others have combined camera trapping and environmental DNA (eDNA) surveys to evaluate changes in species diversity and assemblage composition before and after fire (Magioli et al., 2024). These approaches provide valuable insights, but they are logistically demanding, costly, and generally restricted to specific focal species or limited taxonomic groups. As a result, little is still known about wildlife behavior and persistence during and immediately after fire events across broader assemblages. This gap is largely due to the logistical and ethical challenges of observing animals in real time during wildfires and the inherent difficulty of studying such unpredictable and dangerous events (Zaitsev et al., 2016; Pausas, 2019; Puga et al., 2024).

Here, we present a novel approach by using citizen science data to document animal responses to fire in Brazilian landscapes, offering insights into fire-wildlife interactions across diverse taxa and regions. Specifically, we aim to: (i) analyze the surviving taxonomic groups and their body sizes; (ii) identify potential behavioral survival strategies; and (iii) determine which taxa are most likely to survive and the ecosystem services they provide. We hypothesize that large-bodied and more mobile animals, as well as those that use underground burrows, have greater chances of surviving wildfires.

2. Material and methods

2.1. Database

A database was created using only images voluntarily submitted by firefighters, employees of Brazilian environmental agencies, and researchers involved in wildfire suppression and prescribed burns in Brazil. The photographs, which documented vertebrates impacted by fire, were received by the National Research and Conservation Center for Carnivorous Mammals (CENAP) of the Chico Mendes Institute for Biodiversity Conservation (ICMBio) (Figure 1). Additionally, the dataset included information provided by the non-governmental organization (NGO) Onçafari, the Wild Animal Rehabilitation Center (CRAS) of Mato Grosso do Sul (MS), and images obtained from online news reports on the subject. Images recorded between 2006 and 2024 were considered.

The photographs were organized in a Microsoft Excel spreadsheet, with each row corresponding to an animal impacted by fire. In addition to the images, we compiled information on: i) biome, ii) state, iii) location or name of the Protected Area, iv) fire event type (prescribed burn or wildfire), v) class, vi) order, vii) family, viii) genus, ix) species, and x) body size. Animals were categorized into three body size classes based on their species' average weight: small (less than 1 kg), medium (between 1 kg and 7 kg), and large (more than 7 kg) (Emmons and Feer, 1997; Chiarello, 2000) (Figure 1).

We classified the photographic records based on the type of impact observed. Animals exhibiting visible signs of burns or smoke inhalation, including carcasses, were considered to have suffered a direct impact, as detailed in Pereira et al. (2025). In the present study, we focused on indirect impacts, defined as cases where live animals were recorded in burned areas without apparent injuries. Within this category, we further identified individuals engaged in foraging behavior in the post-fire environment, including scavenging carcasses, hunting live prey, consuming resprouting vegetation, and licking ashes. We also recorded individuals using burrows as shelter in the recently burned landscape.

Whenever possible, animals were identified at the species level. In cases where precise identification was not feasible, at least the order to which they belonged was determined. Identification was based on visual criteria and involved consultation with expert researchers to achieve the lowest possible taxonomic level.

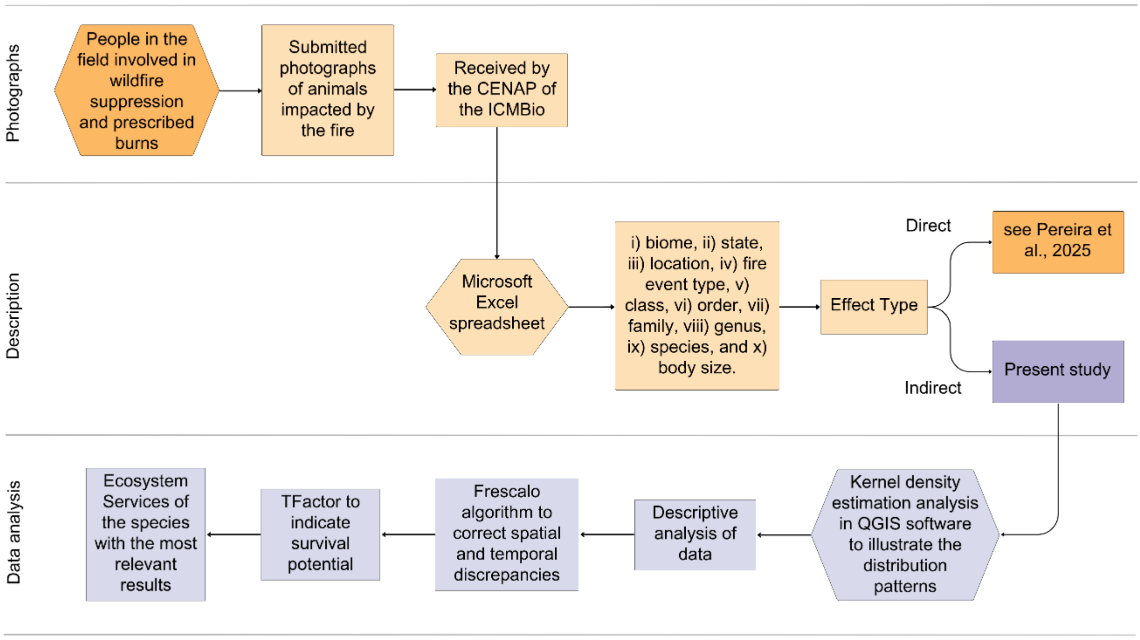


Figure 1: Flowchart representing the methodological steps adopted in the study, from image collection to description. The diagram illustrates the logical sequence of the activities performed.

2.2. Data analysis

A total of 1,133 animals were recorded as indirectly impacted by the fire. To correct estimation biases, a data filtering process was applied. As a result, 16 records lacking initial identification of taxonomic class and fire event type were excluded from the analyses, along with exotic species. Analyses were performed using R software (version 4.4.1). To illustrate the distribution patterns of the received photographs, we conducted a Kernel density estimation analysis in QGIS software (version 3.38.3), using centroids derived from the geographic coordinates of the records.

We applied the Frescalo algorithm (Hill, 2012) to model the data and correct spatial and temporal discrepancies associated with citizen science-based data collection, as it has demonstrated high performance in data analysis (Isaac et al., 2014). The algorithm evaluates observer effort by comparing recorded species with those expected in ecologically similar adjacent regions, calculating standardized local frequencies based on geographic distance and landscape similarity (Hill, 2012). To assess landscape similarity, we used biome classification. When records lacked species-level identification, we considered the highest available taxonomic level.

Based on the Frescalo results, we used the TFactor as a relative measure to assess the temporal frequency of species occurrence, indicating their survival potential. For this analysis, we selected species with low uncertainty in frequency estimates (StDev < 1) and a high TFactor value (> 1), suggesting a greater likelihood of being consistently found over time. The species with the most relevant results were associated with the ecosystem services (ES) they provide, according to Sekercioglu (2006), Valencia-Aguilar et al. (2013), Barbarán (2018), Gaston (2022), Michel et al. (2020), and Vale et al. (2023) (Figure 1).

3. Results

The survey conducted in this study is the first found in the literature to use Citizen Science to account for animals indirectly impacted by fire through photographic records in Brazil. After data filtering, we obtained 1,117 records of animals distributed across five of the six Brazilian biomes over the 18-year sampling period (2006–2024). These results showed that 70.2% of all records were concentrated in the Pantanal biome (784), followed by 23.7% in the Cerrado (265), 3.4% in the Atlantic Forest (38), 2.5% in the Amazon (28), and 0.2% in the Caatinga (2), with no records found for the Pampa (Figure 2). A total of 861 animals (77%) were recorded within Protected Areas (PAs), including Conservation Units and Indigenous Lands, with 535 (47.9%) of them located in privately managed Protected Areas.

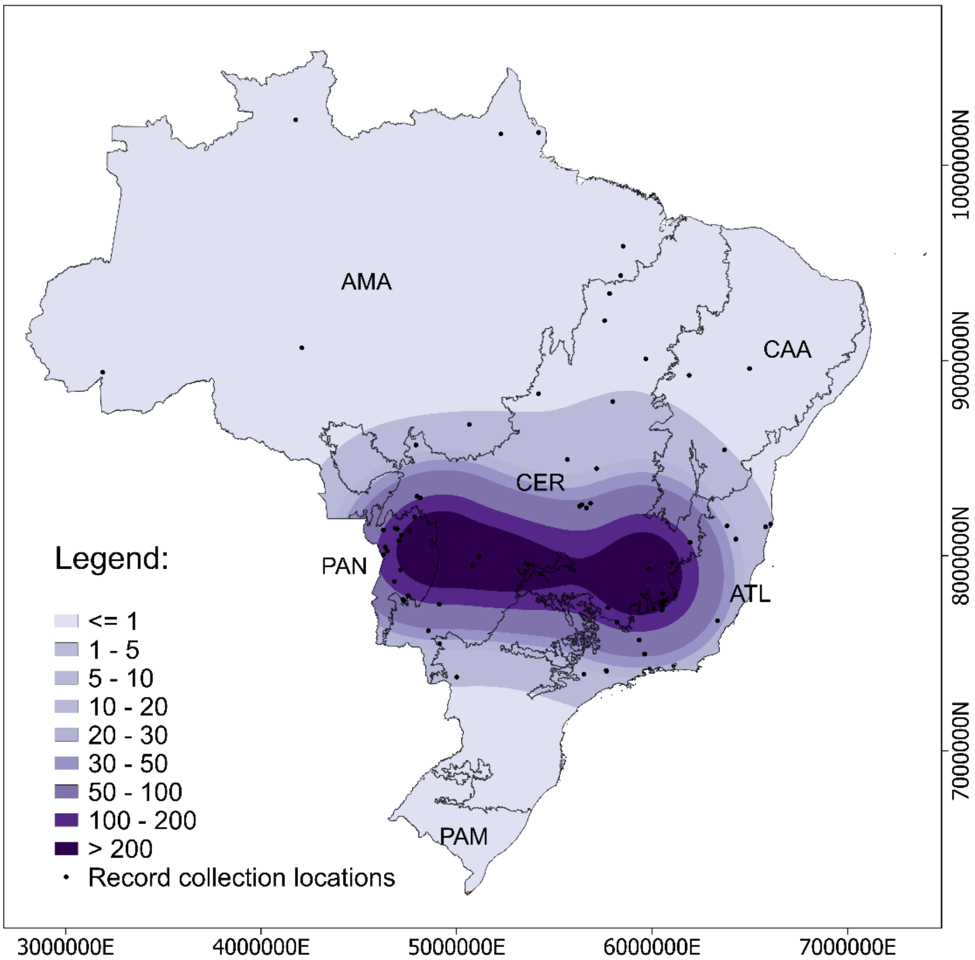


Figure 2: Spatial distribution of the density of records of indirect effects of fire on animals in Brazil. Black lines indicate biome boundaries: AMA – Amazon, ATL – Atlantic Forest, CAA – Caatinga, CER – Cerrado, PAM – Pampa, and PAN – Pantanal.

Fire event records indicated that 88.3% of the data corresponded to wildfires (986) and 11.7% to prescribed burns (131), distributed among amphibians (0.9%), reptiles (12.8%), birds (14.7%), and mammals (71.6%) (Figure 3). Among the records, 35% belonged to the order Artiodactyla (391), 15.5% to Carnivora (173), 11.4% to Squamata (127), and 5.9% to Rodentia (67). Flightless birds (such as Rhea americana) accounted for 4.1% of the records (46). Small, medium, and large body sizes represented 10.8% (121), 28% (313), and 61.1% (683) of the records, respectively.

Regarding families, Cervidae accounted for 26.7% (299) of the records, followed by Felidae with 8.5% (95), Tayassuidae with 8.2% (92), and Canidae with 4.9% (55). At the species level, 87.4% of the records (976) were identified, with Ozotoceros bezoarticus comprising 13.8% (154), Tayassu pecari 7.5% (84), Panthera onca 7% (79), Blastocerus dichotomus 5.9% (66), Subulo gouazoubira 4.9% (55), and Dasyprocta azarae 4.2% (47).

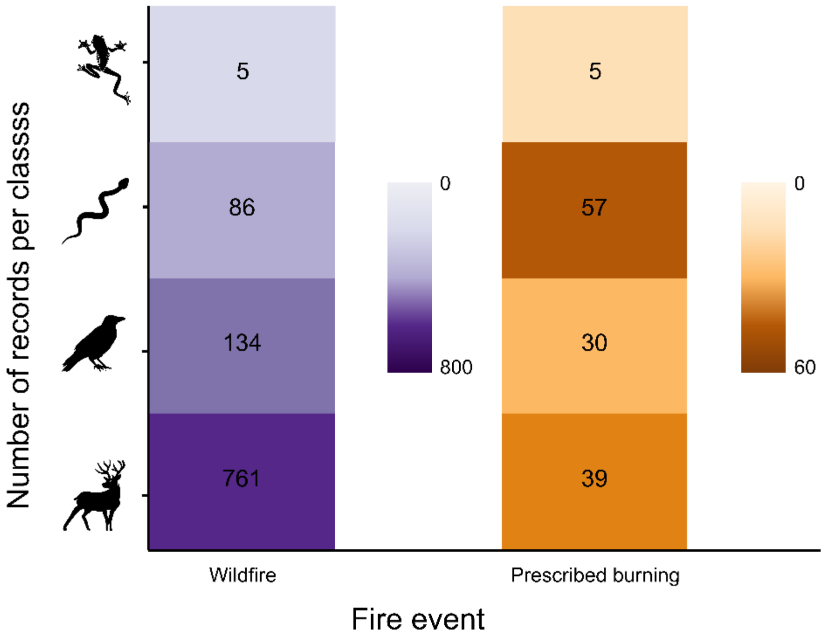


Figure 3: Distribution of the absolute number of records according to the fire event and taxonomic group. On the left axis, the groups are: amphibians, reptiles, birds and mammals.

We classified all records as indirect impacts, encompassing animals observed walking near active fires or within recently burned areas (Figure 4A, B, and D), individuals sheltering in burrows (Figure 4E), and animals foraging in fire-affected environments (Figure 4C and F). Sheltered individuals accounted for 49 records, the majority of which were from the Cerrado biome (31), with Squamata being the most frequently recorded order (31 records). Opportunistic foraging behavior in response to fire was observed in 16.4% of the records (183), with notable occurrences among cervids (69 records; 6.2%) and carnivores (31 records; 2.8%).

Figure 4: Photographs of surviving animals. A) *Panthera onca* (jaguar) individuals walking alongside fire during the 2023 Pantanal wildfire; B) *Chrysocyon brachyurus* (maned wolf) walking in the area recently burned by wildfire in 2010; C) *Caracara plancus* (caracara) preying on a snake during a prescribed burn in 2023; D) *Geranoaetus albicaudatus* (white-tailed hawk) flying in the 2012 wildfire; E) *Philodryas patagoniensis* (papa-pinto) taking refuge in burrows during the 2022 prescribed burn and F) *Ozotoceros bezoarticus* (pampas deer) foraging in recently burned area by wildfire in 2010 (Source: A-B, E-F: CENAP/ICMBio Collection; C: Renan Lieto A. Ribeiro; D: Sávio Freire Bruno).

Finally, the Frescalo results indicated six taxonomic groups with a high relative frequency of temporal occurrence and low uncertainty in the records, suggesting a greater survival potential: Ozotoceros bezoarticus (Tfactor = 2.288; StDev = 0.249), Rhea americana (Tfactor = 2.144; StDev = 0.401), birds (Aves) (Tfactor = 1.892; StDev = 0.388), Didelphidae (Tfactor = 1.329; StDev = 0.835), Myrmecophaga tridactyla (Tfactor = 1.044; StDev = 0.555), and Chelonoidis sp. (Tfactor = 1.038; StDev = 0.834). The class Aves and the family Didelphidae represent cases in which species-level identification was not possible, and therefore, the highest available taxonomic level was considered. Figure 5 associates these taxa with the Ecosystem Services (ES) they provide, with birds performing nine of the eleven ES identified, and cultural services and seed dispersal being the most commonly provided services across taxa.

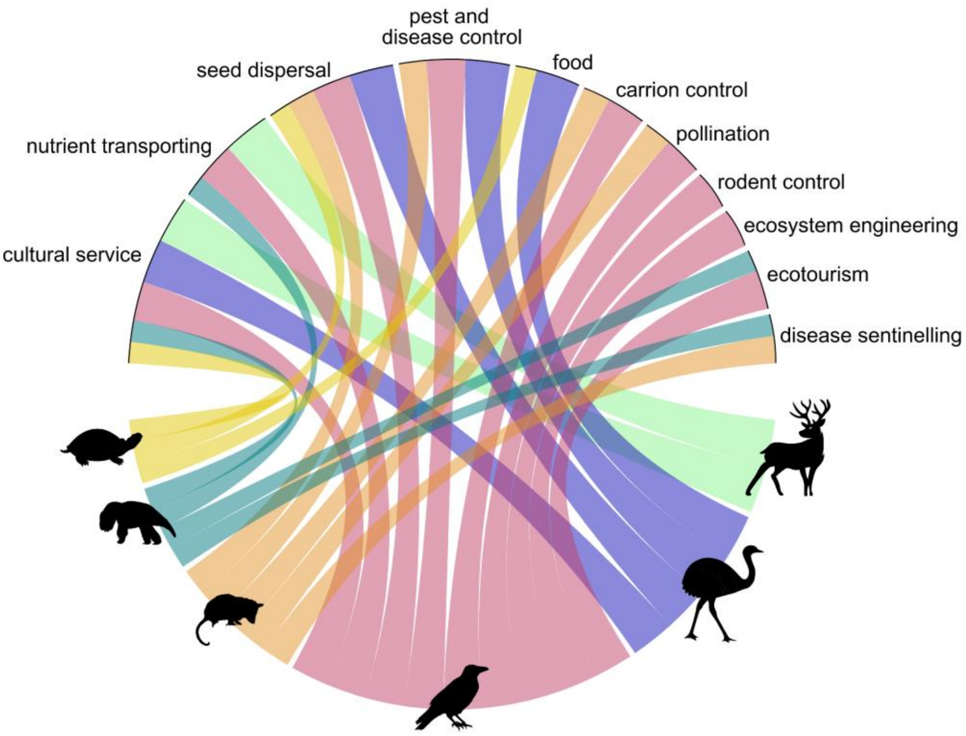


Figura 5: Diagram of species with the most significant Tfactor values, combined with their Ecosystem Services. From right to left, the taxa are: *Chelonoidis sp.*, *Myrmecophaga tridactyla*, Didelphidae, Birds, *Rhea americana* and *Ozotoceros bezoarticus*.

4. Discussion

The analyses conducted in this study revealed that most records were concentrated in the Pantanal biome, followed by the Cerrado. Both biomes are ecologically fire-dependent, exhibiting plant and animal adaptability and resilience (Pivello et al., 2021). This resilience may explain the concentration of animal survival records in these regions. However, it is important to note that these two biomes also encompass the largest burned areas in the country, and therefore, receive the greatest research and monitoring efforts (Pivello et al., 2021; Oliveira et al., 2023). The Pantanal stands out due to extreme droughts and catastrophic fires that have resulted in the death of millions of wild animals (Libonati et al., 2020; Damasceno-Junior et al., 2021; Martins et al., 2022; Pelissari et al., 2023; Brack et al., 2024). Because these extreme events mobilized a larger number of people engaged in firefighting and monitoring activities, they may also have resulted in a higher number of recorded observations.

The limited data from the Amazon and Atlantic Forest, ecosystems sensitive to fire (Pivello et al., 2021), may be explained by the absence of adaptive behaviors to recognize fire cues, leading to more severe direct negative effects such as mortality (Pereira et al., 2025). Individuals of species from fire-adapted habitats that coevolved with fire are more likely to detect its approach and respond effectively, unlike those from habitats that rarely burn, such as tropical rainforests (Nimmo et al., 2021).

The scarcity of data in the Caatinga and Pampa regions may largely reflect the lack of monitoring in these areas. Nevertheless, we still highlight the importance of records from Citizen Science initiatives, which, in many cases, represent the only available source of information on biodiversity. One example is the study by Pereira et al. (2025), which identified the alarming impact of fires on small Brazilian vertebrates and successfully addressed the limitations posed by the absence of consolidated data, helping to avoid duplicated efforts and increased data collection costs.

Regarding differences in records between fire event types, prescribed burns tend to have lower impacts than wildfires, possibly due to their lower combustion efficiency and greater heterogeneity left in the landscape (Volkmann et al., 2020). This heterogeneity may allow less-adapted species to respond positively, especially when compared to more fire-adapted species (Pocknee et al., 2023). In Brazil, prescribed burns are conducted in grassland and savanna environments and are characterized by low-intensity fire, aiming to create vegetation mosaics (Berlinck & Batista, 2020). As such, prescribed burns tends to be less severe than forest wildfires and are unlikely to produce the same effects across different habitats and taxa (Volkmann et al., 2020).

Species indirectly affected by fire exhibit a variety of mechanisms to recover or reoccupy areas following fire-related disturbances. In general, small mammals respond negatively to fire and are sensitive to variations in fire regimes (Andersen, 2021). Pereira et al. (2025) demonstrated that small animals are those that suffer the highest mortality rates. Our findings reflect this pattern, as evidenced by the low detection rate of small-bodied species, while large-bodied mammals appeared more frequently in post-fire records. This may partially reflect greater detectability of larger animals in citizen science photographs, however, it also aligns with previous studies suggesting that larger species tend to be less vulnerable to fire due to their greater mobility, which facilitates escape from fire-affected areas (Batista et al., 2023), a trait similarly observed in birds (Ensbey et al., 2023). Therefore, although detectability might influence the observed pattern, our results reinforce established ecological trends regarding body size and fire survival.

Animal movement plays a critical role in shaping post-fire survival and landscape recolonization. Mobility allows individuals to escape fire-affected areas, seek refuge in unburned patches, and later exploit regenerating habitats (Nimmo et al., 2018). Our findings, which show higher survival rates in large mammals, may be partly explained by their enhanced ability to traverse larger distances and access suitable habitat beyond the fire perimeter. Moreover, recent evidence suggests that post-fire movement patterns are not random; individuals may actively track habitat heterogeneity and resource availability across spatially complex fire mosaics (Gomez et al., 2025).

Our data on foraging animals showed that members of the family Cervidae were the group with the highest number of records. In fire-prone ecosystems, large herbivores may intensively use recently burned areas to access high-quality forage (Magioli et al., 2024). Although Souza et al. (2023) have shown that Ozotoceros bezoarticus appear to use burned and unburned areas with similar intensity, Paemelaere et al. (2024) suggest that these deer may benefit, in the short to medium term after the fire, both from nutrient-rich ash and from the new vegetative regrowth that follows the disturbance. Furthermore, with regard to birds, scavenger species and opportunists, such as vultures and caracaras, are often seen foraging in burned areas, taking advantage of the increased visibility of weakened prey or the availability of carcasses (Pausas & Parr, 2018).

In our dataset, we identified individuals sheltering in burrows shortly after fire events, suggesting that the use of subterranean refuges may be an important survival strategy. A notable example supporting this behavior is the observation of living individuals of the marsh rat (Holochilus chacarius) inside partially flooded underground burrows following the 2020 megafires in the Pantanal (Semedo et al., 2022). This finding reinforces that animals observed sheltering in our study, particularly in the Cerrado biome, may possess similar behavioral adaptations. Burrows and other belowground refuges are generally cooler than the surrounding environment, offering thermal buffering during extreme aboveground temperatures (Di Blanco et al., 2020). Moreover, the use of such structures is broadly associated with a range of ecological functions, including thermoregulation, predator avoidance, nesting, and protection from environmental disturbances (Di Blanco et al., 2020; Haussmann et al., 2023; Santos et al., 2025). In the Brazilian Cerrado, the absence of lizard mortality following fires was attributed to the use of refuges such as burrows and termite mounds, where individuals were directly located during post-fire surveys (Costa et al., 2013).

Some studies suggest that the herpetofauna of fire-prone ecosystems may be relatively well adapted to natural fire regimes, exhibiting traits and behaviors that facilitate persistence in fire-affected landscapes, like the excavation (Piliod et al., 2003; Drummond et al., 2018). Reptile responses to fire reveal complex patterns of resilience and vulnerability. Squamate reptiles face significant threats from fire, particularly from inappropriate fire regimes (Santos et al., 2022), due to their physiology being highly sensitive to environmental changes (Doherty et al., 2020). However, reptiles inhabiting early-successional habitats (open fields) often include saxicolous and fossorial species (Santos et al., 2016), which may enhance their survival during fire events. Thermoregulatory strategies, such as the ability to modulate body temperature in response to environmental conditions, may also confer some resilience to fire (Bícego, 2020), but effective shelter availability remains a key determinant of survival. Lizards sheltered in burrows or termite mounds have been observed to survive fire (Costa et al., 2013; Atkins et al., 2015), whereas species lacking such refuges may experience extensive mortality (Tomas et al., 2021; Pereira et al., 2025).

From an ecosystem functional perspective, animals play a key role in the success of environmental restoration by facilitating the dispersal of pollen, seeds, and microorganisms necessary for recovery (Bello et al., 2024). The association between taxa with higher survival estimates and their ecosystem services revealed that Rhea americana, birds, and the family Didelphidae provide seed dispersal services; in addition, the latter two also contribute to pollination. Seed dispersal and pollination may play essential roles in the recolonization of burned areas. Similarly, refugia serve as dispersal sources for surviving species, enabling ecosystem reassembly following disturbance (Robinson et al., 2013).

Moreover, fire can influence predator-prey interactions by rapidly altering the distribution of cover and food resources (Jorge et al., 2020). Predators may benefit from fire in the short term due to increased hunting success in simplified landscapes (Doherty et al., 2022). While many predators do not exhibit a clear and consistent response to fire, there are instances where fire shapes their spatial distribution, diet, hunting success, and competitive interactions, intensifying predation pressure in fire-prone ecosystems (Geary et al., 2020).

5. Conclusion

The results of this study indicate that large mammals exhibited the highest survival rates, corroborating the hypothesis. The use of burrows represented an important strategy for fire survival, especially for scaly reptiles. Ozotoceros bezoarticus, Rhea americana, birds, Didelphidae, Myrmecophaga tridactyla and Chelonoidis spp. were the taxa with the highest survival potential. R. americana, birds, and Didelphidae provide the ecosystem service of seed dispersal, which may be essential for recolonizing burned areas.

Importantly, this study provides a national-scale overview of animal survival in response to fire, which should serve as a foundation for further research and monitoring at regional and local scales, thereby bridging current knowledge gaps in fire ecology across Brazil. Future efforts should prioritize the creation of a standardized database on fire-related animal mortality and survival, ensuring data comparability across biomes and taxa. Likewise, the adoption of capture–recapture approaches and other demographic tools would allow robust estimates of survival and population resilience under different fire regimes. Beyond these recommendations, it is essential to increase community engagement in scientific knowledge-building by strengthening citizen science initiatives and incorporating local ecological knowledge. Citizen participation not only expands monitoring capacity but also enhances the societal relevance of fire management strategies.

Recognizing that fire inevitably generates winners and losers among species, management actions must be planned, monitored, and adaptively revised to achieve biodiversity conservation goals. To promote environmental heterogeneity and support biodiversity conservation in fire-prone ecosystems, we recommend the implementation of mosaic landscape management through the strategic use of prescribed burns.

Acknowledgements

The authors acknowledge the financial support provided by the Coordination for the Improvement of Higher Education Personnel (CAPES - financing code 001) and National Council for Scientific and Technological Development (CNPq) for the scholarship granted to A. R. Pereira (this article is a part of her Master's research) and through the funding of the project 'Efeitos do fogo sobre a abundância e diversidade de vertebrados do Parque Nacional da Serra da Canastra' CNPq/MCTI/FNDCT No. 18/2021, process nº 406473/2021-8. We would also like to thank the ONG Onçafari, which kindly provided its field data, and all those who gathered and recorded field data and kindly provided us with the images. We would also like to thank the firefighters, managers and people directly involved in firefighting and carrying out the prescribed burning. Finally, we would like to thank the identification experts for their

collaboration in identifying many animals.

Database

Pereira, A. R., Torres, F. T. P., Berlinck, C. N., 2025. Indirect Impacts of Fire on Vertebrates [dataset]. Mendeley Data, V1. https://doi.org/10.17632/rgg4538296.1

References

Andersen, A. N. (2021). Faunal responses to fire in Australian tropical savannas: insights from field experiments and their lessons for conservation management. *Diversity and Distributions*, *27*(5), 828-843. https://doi.org/10.1111/ddi.13198

Atkins, Z., Clemann, N., & Robert, K. A. (2015). Does shelter site selection aid persistence of a threatened alpine lizard? Assessing Liopholis guthega populations a decade after severe fire in southeastern Australia. *Journal of Herpetology*, *49*(2), 222-229. https://doi.org/10.1670/13-194

Banks, S. C., Dujardin, M., McBurney, L., Blair, D., Barker, M., & Lindenmayer, D. B. (2011). Starting points for small mammal population recovery after wildfire: recolonisation or residual populations?. *Oikos*, *120*(1), 26-37. https://doi.org/10.1111/j.1600-0706.2010.18765.x

Banks, S. C., McBurney, L., Blair, D., Davies, I. D., & Lindenmayer, D. B. (2017). Where do animals come from during post-fire population recovery? Implications for ecological and genetic patterns in post-fire landscapes. *Ecography*, *40*(11), 1325-1338. https://doi.org/10.1111/ecog.02251

Barbarán, F. R. (2018). Comercio de cueros y plumas de Rheiformes *Rhea americana* y *Rhea pennata* en la Provincia de Salta, Argentina. *Revista Biodiversidad Neotropical*, *8*(2), 128-143.

Batista, E. K., Figueira, J. E., Solar, R. R., de Azevedo, C. S., Beirão, M. V., Berlinck, C. N., ... & Fernandes, G. W. (2023). In case of fire, escape or die: a trait-based approach for identifying animal species threatened by fire. *Fire*, *6*(6), 242. https://doi.org/10.3390/fire6060242

Bello, C., Dent, D. H., & Crowther, T. W. (2024). Animals in restoration to achieve climate biodiversity targets. *Trends in Ecology & Evolution*. https://doi.org/10.1016/j.tree.2024.08.011

Berlinck, C. N., & Batista, E. K. (2020). Good fire, bad fire: It depends on who burns. *Flora*, *268*, 151610. https://doi.org/10.1016/j.flora.2020.151610

Bícego, K. C. (2020). Ectotermia e endotermia. In *Fisiologia Térmica de Vertebrados*. Cultura Acadêmica, São Paulo, ISBN 978-85-7249-066-5, pp. 69–87.

Brack, I. V., Cordeiro, J. L., Kindel, A., Rangel, B. Z., Crawshaw, D., Heiermann, D., ... & de Oliveira, L. F. (2024). Spatial modelling and estimation of mammals' mortalities by Pantanal

2020 megafires. *Journal of Applied Ecology*, *61*(11), 2848-2859. https://doi.org/10.1111/1365-2664.14789

Collins, L., Bennett, A. F., Leonard, S. W., & Penman, T. D. (2019). Wildfire refugia in forests: Severe fire weather and drought mute the influence of topography and fuel age. *Global Change Biology*, *25*(11), 3829-3843. https://doi.org/10.1111/gcb.14735

Costa, B. M., Pantoja, D. L., Vianna, M. C. M., & Colli, G. R. (2013). Direct and short-term effects of fire on lizard assemblages from a Neotropical savanna hotspot. *Journal of Herpetology*, *47*(3), 502-510. https://doi.org/10.1670/12-043

Damasceno-Junior, G. A., Pereira, A. D. M. M., Oldeland, J., Parolin, P., & Pott, A. (2022). Fire, flood and Pantanal vegetation. In *Flora and Vegetation of the Pantanal wetland* (pp. 661-688). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-030-83375-6_18

Di Blanco, Y. E., Desbiez, A. L., Di Francescantonio, D., & Di Bitetti, M. S. (2020). Excavations of giant armadillos alter environmental conditions and provide new resources for a range of animals. *Journal of Zoology*, *311*(4), 227-238. https://doi.org/10.1111/jzo.12782

Doherty, T. S., Balouch, S., Bell, K., Burns, T. J., Feldman, A., Fist, C., ... & Driscoll, D. A. (2020). Reptile responses to anthropogenic habitat modification: A global meta-analysis. *Global Ecology and Biogeography*, *29*(7), 1265-1279. https://doi.org/10.1111/geb.13091

Doherty, T. S., Geary, W. L., Jolly, C. J., Macdonald, K. J., Miritis, V., Watchorn, D. J., ... & Dickman, C. R. (2022). Fire as a driver and mediator of predator–prey interactions. *Biological Reviews*, *97*(4), 1539-1558. https://doi.org/10.1111/brv.12853

Drummond, L. O., Moura, F. R., & Pires, M. R. S. (2018). Impact of fire on anurans of rupestrian grasslands (campos rupestres): a case study in the Serra do Espinhaço, Brazil. *Salamandra*, 54(1).

Einoder, L. D., Fisher, A., Hill, B. M., Buckley, K., de Laive, A. H., Woinarski, J. C. Z., & Gillespie, G. R. (2023). Long term monitoring reveals the importance of large, long unburnt areas and smaller fires in moderating mammal declines in fire-prone Savanna of northern Australia. *Journal of Applied Ecology*, *60*(10), 2251-2266. https://doi.org/10.1111/1365-2664.14482

Engstrom, R. T. (2010). First-order fire effects on animals: review and recommendations. *Fire Ecology*, *6*, 115-130. https://doi.org/10.4996/fireecology.0601115

Ensbey, M., Legge, S., Jolly, C. J., Garnett, S. T., Gallagher, R. V., Lintermans, M., ... & Zukowski, S. (2023). Animal population decline and recovery after severe fire: Relating ecological and life history traits with expert estimates of population impacts from the Australian 2019-20 megafires. *Biological Conservation*, *283*, 110021. https://doi.org/10.1016/j.biocon.2023.110021

Gaston, K. J. (2022). Birds and ecosystem services. *Current Biology*, *32*(20), R1163-R1166. https://doi.org/10.1016/j.cub.2022.07.053

Geary, W. L., Doherty, T. S., Nimmo, D. G., Tulloch, A. I., & Ritchie, E. G. (2020). Predator responses to fire: A global systematic review and meta-analysis. *Journal of Animal Ecology*, *89*(4), 955-971. https://doi.org/10.1111/1365-2656.13153

Gomez, S., English, H. M., Bejarano Alegre, V., Blackwell, P. G., Bracken, A. M., Bray, E., ... & Börger, L. (2025). Understanding and predicting animal movements and distributions in the Anthropocene. *Journal of Animal Ecology*. https://doi.org/10.1111/1365-2656.70040

Hale, S., Mendoza, L., Yeatman, T., Cooke, R., Doherty, T., Nimmo, D., & White, J. G. (2022). Evidence that post-fire recovery of small mammals occurs primarily via in situ survival. *Diversity and Distributions*, *28*(3), 404-416. https://doi.org/10.1111/ddi.13283

Haussmann, N. S., Blomsterberg-Reyneke, S. E., le Roux, P. C., McIntyre, T., & Bennett, N. C. (2023). Multi-Species Visits to an Aardvark Burrow–Whose Turn Is It Next?. *African Journal of Wildlife Research*, *53*(1). https://doi.org/10.3957/056.053.0006

He, T., Lamont, B. B., & Pausas, J. G. (2019). Fire as a key driver of Earth's biodiversity. *Biological Reviews*, *94*(6), 1983-2010. https://doi.org/10.1111/brv.12544

Hill, M. O. (2012). Local frequency as a key to interpreting species occurrence data when recording effort is not known. *Methods in Ecology and Evolution*, *3*(1), 195-205. https://doi.org/10.1111/j.2041-210X.2011.00146.x

Isaac, N. J., van Strien, A. J., August, T. A., de Zeeuw, M. P., & Roy, D. B. (2014). Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution*, *5*(10), 1052-1060. https://doi.org/10.1111/2041-210X.12254

Jolly, C. J., Dickman, C. R., Doherty, T. S., van Eeden, L. M., Geary, W. L., Legge, S. M., ... & Nimmo, D. G. (2022). Animal mortality during fire. *Global Change Biology*, *28*(6), 2053-2065. https://doi.org/10.1111/gcb.16044

Jorge, M. H., Garrison, E. P., Conner, L. M., & Cherry, M. J. (2020). Fire and land cover drive predator abundances in a pyric landscape. *Forest Ecology and Management*, *461*, 117939. https://doi.org/10.1016/j.foreco.2020.117939

Libonati, R., DaCamara, C. C., Peres, L. F., Sander de Carvalho, L. A., & Garcia, L. C. (2020). Rescue Brazil's burning Pantanal wetlands. *Nature*, *588*(7837), 217-219. https://doi.org/10.1038/d41586-020-03464-1

Martins, P. I., Belém, L. B. C., Szabo, J. K., Libonati, R., & Garcia, L. C. (2022). Prioritising areas for wildfire prevention and post-fire restoration in the Brazilian Pantanal. *Ecological Engineering*, *176*, 106517. https://doi.org/10.1016/j.ecoleng.2021.106517

Magioli, M., Lima, L. H. A., Villela, P. M. S., Sampaio, R., Bonjorne, L., Ribeiro, R. L. A., ... & Berlinck, C. N. (2024). Forest type modulates mammalian responses to megafires. *Scientific Reports*, *14*(1), 13538. https://doi.org/10.1038/s41598-024-64460-3

McLauchlan, K. K., Higuera, P. E., Miesel, J., Rogers, B. M., Schweitzer, J., Shuman, J. K., ... & Watts, A. C. (2020). Fire as a fundamental ecological process: Research advances and frontiers. *Journal of Ecology*, *108*(5), 2047-2069. https://doi.org/10.1111/1365-2745.13403

Mendyk, R. W., Weisse, A., & Fullerton, W. (2020). A wake-up call for sleepy lizards: the olfactory-driven response of Tiliqua rugosa (Reptilia: Squamata: Sauria) to smoke and its implications for fire avoidance behavior. *Journal of Ethology*, *38*(2), 161-166. https://doi.org/10.1007/s10164-019-00628-z

Michel, N. L., Whelan, C. J., & Verutes, G. M. (2020). Ecosystem services provided by Neotropical birds. *The Condor*, *122*(3), duaa022. https://doi.org/10.1093/condor/duaa022

Moritz, M. A., Batllori, E., & Bolker, B. M. (2023). The role of fire in terrestrial vertebrate richness patterns. *Ecology Letters*, *26*(4), 563-574. https://doi.org/10.1111/ele.14177

Nimmo, D. G., Avitabile, S., Banks, S. C., Bliege Bird, R., Callister, K., Clarke, M. F., ... & Bennett, A. F. (2019). Animal movements in fire-prone landscapes. *Biological Reviews*, *94*(3), 981-998. https://doi.org/10.1111/brv.12486

Nimmo, D. G., Carthey, A. J., Jolly, C. J., & Blumstein, D. T. (2021). Welcome to the Pyrocene: Animal survival in the age of megafire. *Global Change Biology*, *27*(22), 5684-5693. https://doi.org/10.1111/gcb.15834

Nowack, J., Delesalle, M., Stawski, C., & Geiser, F. (2016). Can hibernators sense and evade fires? Olfactory acuity and locomotor performance during deep torpor. *The Science of Nature*, *103*(9), 1-7. https://doi.org/10.1007/s00114-016-1396-6

Oliveira, U., Soares-Filho, B., Rodrigues, H., Figueira, D., Gomes, L., Leles, W., ... & Miranda, H. (2023). A near real-time web-system for predicting fire spread across the Cerrado biome. *Scientific Reports*, *13*(1), 4829. https://doi.org/10.1038/s41598-023-30560-9

Paemelaere, EA, Hallett, MT, de Freitas, K., Balvadore, S., Ignace, M., Mandook, A., ... & van Vliet, N. (2025). Medium and large mammal responses to fire in a neotropical savanna system in Guyana. *Biotropica*, 57(1), e13397. https://doi.org/10.1111/btp.13397

Pausas, J. G. (2019). Generalized fire response strategies in plants and animals. *Oikos*, *128*(2), 147-153. https://doi.org/10.1111/oik.05907

Pausas, J. G., & Parr, C. L. (2018). Towards an understanding of the evolutionary role of fire in animals. *Evolutionary Ecology*, *32*(2), 113-125. https://doi.org/10.1007/s10682-018-9927-6

Pelissari, T. D., Teodoro, P. E., Teodoro, L. P. R., Lima, M., Santana, D. C., Rossi, F. S., ... & da Silva Junior, C. A. (2023). Dynamics of major environmental disasters involving fire in the Brazilian Pantanal. *Scientific Reports*, *13*(1), 21669. https://doi.org/10.1038/s41598-023-49154-6

Pereira, A. R., Torres, F. T. P., & Berlinck, C. N. (2025). Ecological implications of the direct effects of fire on neotropical vertebrates. *Science of The Total Environment*, *979*, 179437. https://doi.org/10.1016/j.scitotenv.2025.179437

Pilliod, D. S., Bury, R. B., Hyde, E. J., Pearl, C. A., & Corn, P. S. (2003). Fire and amphibians in North America. *Forest Rcology and Management*, *178*(1-2), 163-181. https://doi.org/10.1016/S0378-1127(03)00060-4

Pivello, V. R., Vieira, I., Christianini, A. V., Ribeiro, D. B., da Silva Menezes, L., Berlinck, C. N., ... & Overbeck, G. E. (2021). Understanding Brazil's catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. *Perspectives in Ecology and Conservation*, *19*(3), 233-255. https://doi.org/10.1016/j.pecon.2021.06.005

Pocknee, C. A., Legge, S. M., McDonald, J., & Fisher, D. O. (2023). Modeling mammal response to fire based on species' traits. *Conservation Biology*, *37*(4), e14062. https://doi.org/10.1111/cobi.14062

Puga, J. R., Abrantes, N. J., Moreira, F., & Keizer, J. J. (2024). Short-term impacts of wildfires on the diversity and activity patterns of medium-sized mammals in mediterranean coastal pine forests. *Forest Ecology and Management*, *562*, 121940. https://doi.org/10.1016/j.foreco.2024.121940

Rego, F. C., Morgan, P., Fernandes, P., Hoffman, C., Castro Rego, F., Morgan, P., ... & Hoffman, C. (2021). Fire effects on plants, soils, and animals. In *Fire science: From chemistry to landscape management*, 259-318. https://doi.org/10.1007/978-3-030-69815-7_9

Ribeiro, A. C. D. C., Ortega, J. C., Bini, L. M., Ferro, V. G., Bispo, A. A., Carvalho, W. F., ... & Cianciaruso, M. V. (2025). The effect of fire on the structure of animal metacommunities in a Cerrado landscape: A 10-year survey of anurans, birds and moth assemblages. *Journal for Nature Conservation*, 126856. https://doi.org/10.1016/j.jnc.2025.126856

Robinson, N. M., Leonard, S. W., Ritchie, E. G., Bassett, M., Chia, E. K., Buckingham, S., ... & Clarke, M. F. (2013). Refuges for fauna in fire-prone landscapes: their ecological function and importance. *Journal of Applied Ecology*, *50*(6), 1321-1329. https://doi.org/10.1111/1365-2664.12153

Santos, F. M., Sano, N. Y., de Assis, W. O., Nascimento, L. F., de Oliveira, J., Fonseca, C., ... & de Oliveira Porfirio, G. E. (2024). Armadillo burrows: a meeting point for biodiversity in the Pantanal Wetland. *Mammalian Biology*, 1-8. https://doi.org/10.1007/s42991-024-00466-8

Santos, J. L., Sitters, H., Keith, D. A., Geary, W. L., Tingley, R., & Kelly, L. T. (2022). A demographic framework for understanding fire-driven reptile declines in the 'land of the lizards'. *Global Ecology and Biogeography*, *31*(10), 2105-2119. https://doi.org/10.1111/geb.13520

Santos, X., Badiane, A., & Matos, C. (2016). Contrasts in short-and long-term responses of Mediterranean reptile species to fire and habitat structure. *Oecologia*, *180*, 205-216. https://doi.org/10.1007/s00442-015-3453-9

Santos, X., Belliure, J., Gonçalves, J. F., & Pausas, J. G. (2022). Resilience of reptiles to megafires. *Ecological Applications*, *32*(2), e2518. https://doi.org/10.1002/eap.2518

Semedo, T. B. F., Libardi, G. S., Strüssmann, C., Berlinck, C. N., Tomas, W. M., & Garbino, G. S. T. (2022). Discovery of underground shelters occupied by the Chacoan Marsh Rat after massive wildfires in Pantanal, Brazil. *Therya Notes*, *3*, 30-35. https://doi.org/10.12933/therya_notes-22-65

Sekercioglu, C. H. (2006). Increasing awareness of avian ecological function. *Trends in Ecology & Evolution*, *21*(8), 464-471. https://doi.org/10.1016/j.tree.2006.05.007

Shaw, R. E., James, A. I., Tuft, K., Legge, S., Cary, G. J., Peakall, R., & Banks, S. C. (2021). Unburnt habitat patches are critical for survival and in situ population recovery in a small mammal after fire. *Journal of Applied Ecology*, *58*(6), 1325-1335. https://doi.org/10.1111/1365-2664.13846

Souza, C. V., Lourenço, Á., & Vieira, E. M. (2023). Species-specific responses of medium and large mammals to fire regime attributes in a fire-prone neotropical savanna. *Fire*, *6*(3), 110. https://doi.org/10.3390/fire6030110

Tomas, W. M., Berlinck, C. N., Chiaravalloti, R. M., Faggioni, G. P., Strüssmann, C., Libonati, R., ... & Morato, R. (2021). Distance sampling surveys reveal 17 million vertebrates directly killed by the 2020's wildfires in the Pantanal, Brazil. *Scientific Reports*, *11*(1), 23547. https://doi.org/10.1038/s41598-021-02844-5

Vale, M. M., Vieira, M. V., Grelle, C. E. V., Manes, S., Pires, A. P., Tardin, R. H., ... & Tourinho, L. (2023). Ecosystem services delivered by Brazilian mammals: spatial and taxonomic patterns and comprehensive list of species. *Perspectives in Ecology and Conservation*, *21*(4), 302-310. https://doi.org/10.1016/j.pecon.2023.10.003

Valencia-Aguilar, A., Cortés-Gómez, A. M., & Ruiz-Agudelo, C. A. (2013). Ecosystem services provided by amphibians and reptiles in Neotropical ecosystems. *International Journal of Biodiversity Science, Ecosystem Services & Management*, *9*(3), 257-272. https://doi.org/10.1080/21513732.2013.821168

Volkmann, L. A., Hutchen, J., & Hodges, K. E. (2020). Trends in carnivore and ungulate fire ecology research in North American conifer forests. *Forest Ecology and Management*, *458*, 117691. https://doi.org/10.1016/j.foreco.2019.117691

CHAPTER 3

Subterranean Shelters Utilization by Vertebrates as an Adaptation to Fire Survival in Serra da Canastra National Park, Brazil

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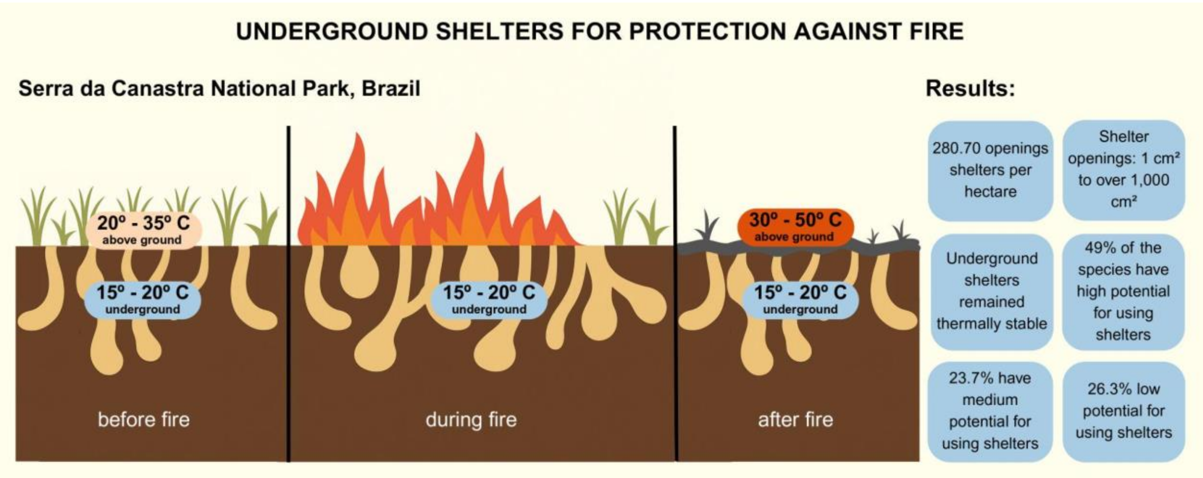
Manuscript submitted to the Journal *Biological Conservation.*

Highlights:

- Serra da Canastra National Park (SCNP) provides a functional network of underground shelters;
- Shelter openings ranging from 1 cm² to over 1,000 cm²;
- Underground shelters remained thermally stable during and after fire events;
- 49% of the species analyzed in the SCNP have high potential for using underground shelters for protection against fire.

Graphical Abstract:



Abstract: Refuges are habitat features that increase organisms' chances of survival during and immediately after fires, and they can occur at multiple spatial scales. In this study, we assessed the availability of underground shelter openings and their potential as protection for vertebrate fauna against fire in the grassland environments of Serra da Canastra National Park (SCNP). We applied an adapted distance sampling technique to estimate the density of these openings, measured their areas, and compared internal and external temperatures before and after fire events. The estimates indicated approximately 280.7 openings per hectare in the grasslands of SCNP. Temperatures inside the shelters were significantly lower than external temperatures before and after the fire. We also estimated the potential use of these shelters by 192 species in the Park, of which 49% showed high or very high potential for use. Our results consistently indicate that these underground structures play a key role in protecting grassland fauna in the Cerrado during fire events.

Keywords: Ecological learning; Refuges; Burrows; Wildfire; Prescribed burn; Brazilian savanna.

1. Introduction

Fire has shaped the structure, function, and composition of terrestrial ecosystems for millions of years (Jolly et al., 2015; He et al., 2019; Pivello et al., 2021). However, the increasing frequency and intensity of wildfires (Wu et al., 2021) now threaten ecological integrity and are pushing ecosystems toward extremes resilience thresholds (Kelly et al., 2020). These changes challenge the adaptive mechanisms of species in response to fire disturbances, mechanisms that are largely determined by their ecological traits and life-history strategies (Souza et al., 2023; Pocknee et al., 2023). In animals, the effects of fire can be classified as: (i) direct, when fire causes mortality (Tomas et al., 2021); (ii) indirect, when it leads to habitat alterations, reduced resource availability, or increased predation rates (Doherty et al., 2022; Magioli et al., 2024); and (iii) evolutionary, when it acts as a selective force favoring adaptive traits over the long term (Engstrom, 2010).

The evolutionary effects of fire are most evident in ecosystems prone to this type of disturbance. In these environments, many species exhibit structural and phenotypic traits that, although not direct adaptations to fire, may provide advantages for survival during and after vegetation fires (Pausas & Parr, 2018). These structural and behavioral traits include, for example, the ability to recognize olfactory, auditory, and visual cues associated with fire, which trigger protective responses that increase individual survival chances (Nimmo et al., 2021; Jolly et al., 2022). In some hibernators, the detection of smoke during torpor induces arousal and escape to safer locations (Nowack et al., 2016). Lizards, in turn, can detect smoke compounds through tongue-flick behavior, which elicits escape responses (Mendyk et al., 2020; Álvarez-Ruiz et al., 2021). Large-bodied, highly mobile species, such as deer, typically respond to fire by rapidly fleeing affected areas (Pereira et al., 2025a *unpublished results*). In addition to fleeing, many animals seek refuge in non-flammable shelters, such as burrows, deep crevices, bodies of water, or adjacent vegetation that is less vulnerable to fire (Nimmo et al., 2021).

Thus, structural elements of the habitat, such as forest patches, logs, burrows, and rocky outcrops, are essential for protecting animals from the direct impacts of fire by providing refuge at different scales and functioning as potential nuclei for area recovery (Hale et al., 2022). Following a wildfire in the Brazilian Pantanal, several animals were observed emerging from underground refuges shortly after the fire had passed (Semedo et al., 2022a). In the same event, the use of underground structures by the Chaco marsh rat during the fire was reported for the first time (Semedo et al., 2022b). In a study conducted in the Brazilian Cerrado, the absence of lizard mortality following fire was attributed to the use of shelters such as burrows and termite mounds, where individuals were located during post-fire surveys (Costa et al., 2013).

In Brazil, fire plays different ecological roles across the landscape, particularly in biomes such as the Cerrado, Pampa, and Pantanal, which have a strong ecological and evolutionary history associated with fire (Pivello et al., 2021). The Cerrado in particular, a biodiversity hotspot composed of a mosaic of grasslands, savannas, and forests, can benefit from pyrodiversity, a concept that describes how different fire regimes can promote biological diversity (Martin & Sapsis, 1992; Steel et al., 2023). As a result, Cerrado fauna is considered less susceptible to the direct effects of fire, both due to evolutionary adaptations accumulated over time and to population characteristics, such as lower population densities, which may reduce exposure to fire compared to environments where denser populations experience higher mortality rates (Pereira et al., 2025b).

For many years, the Cerrado was threatened by consistent fire suppression policies, and most protected areas followed total fire exclusion strategies (Durigan & Ratter, 2016), which led to the accumulation of fine fuels and the occurrence of large, destructive wildfires (Schmidt et al., 2018). However, local communities have long used fire to manage landscapes for cultivation, plant harvesting, hunting, and cattle grazing (Moura et al., 2019; Levis et al., 2024; Novato et al., 2025), and, together with natural fires (Durigan, 2020), these practices create mosaic burn patterns that can help prevent the spread of large wildfires (Franke et al., 2024).

Refuges can occur at multiple spatial scales, from microhabitats to structural elements at the landscape level, such as gallery forests, and at different temporal scales, being either temporary or permanent features in the landscape. They are defined as habitat features that facilitate the survival of organisms during and immediately after a fire event, enable the in situ persistence of populations within the burned area, and contribute to population recovery as the area regenerates, thus playing a crucial role in sustaining species and communities (Robinson et al., 2013).

In this study, we focused on the openings of underground shelters and estimated their potential availability as protection for vertebrate fauna against fire in the grassland environments of Serra da Canastra National Park. Our objectives were: (i) to assess temperature changes inside the shelters during fire passage in order to highlight their importance both during the fire and in the immediate post-fire period, when external conditions become inhospitable; and (ii) to infer which animal groups are capable of using these shelters, based on their habits. We hypothesized that underground shelters may act as important protective structures, with the potential to reduce fauna mortality during fires in the Cerrado.

2. Material and Methods

2.1 Study area

This study was conducted in grassland formations of Serra da Canastra National Park (SCNP), located in the state of Minas Gerais, southeastern Brazil (20º 18' 16" S and 46º 35' 56" W). The Park is a protected area covering 197,900 hectares (ha) of Cerrado, situated within the municipalities of Capitólio, Delfinópolis, Sacramento, São João Batista do Glória, São Roque de Minas, and Vargem Bonita (ICMBio, 2023). The territory is characterized by conflicts of interest between the Park and the local community, which is known for its agricultural and livestock activities carried out on private properties located in unregularised areas (Batista et al., 2018). The native grasslands are managed with fire by the community for the production of Canastra cheese and agriculture. This scenario highlights the challenges of reconciling environmental conservation with traditional productive practices in the region (ICMBio, 2023).

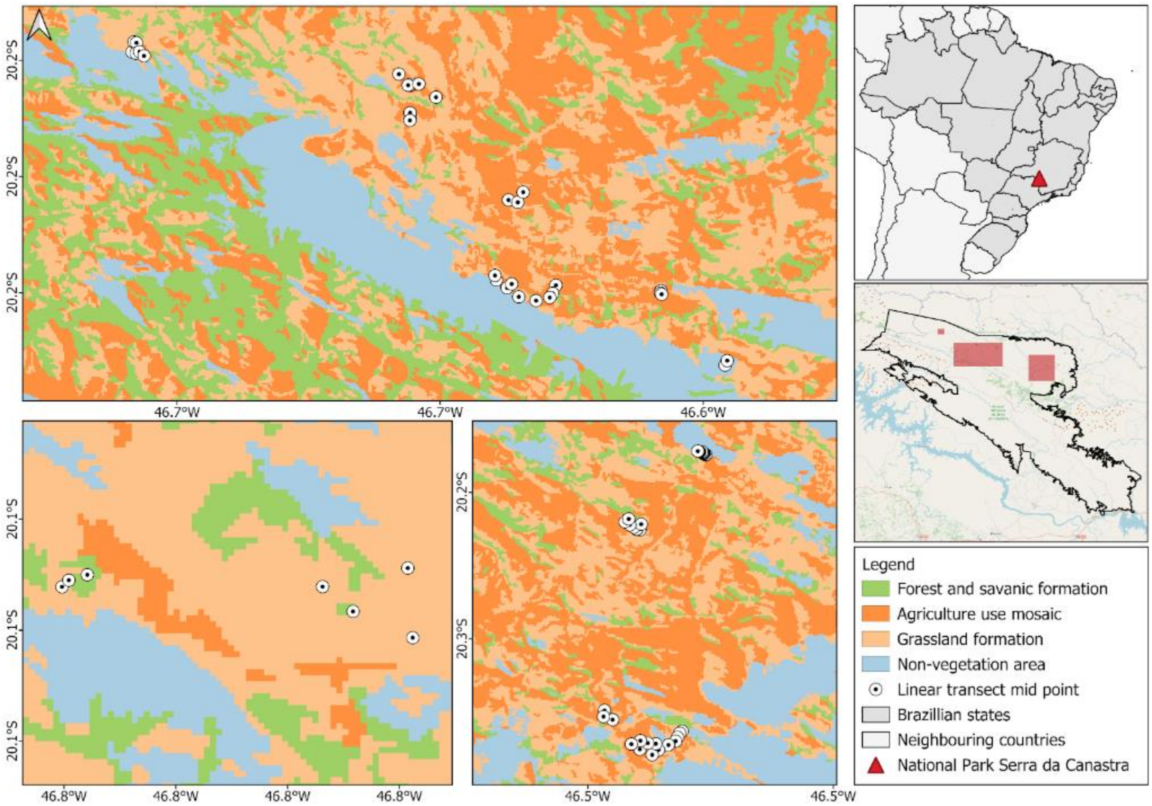


Figure 1: Location of Serra da Canastra National Park in Brazil and central location of transects. Land cover was obtained and grouped from the MapBiomas project (https://brasil.mapbiomas.org/).

The landscape of SCNP is predominantly composed of grassland formations of the Cerrado, which include three different phytophysiognomies*:* *campo sujo*, *campo rupestre*, and *campo limpo*. The park also encompasses savanna formations classified as *cerrado sensu stricto*, which comprise dense cerrado, sparse cerrado, and rocky cerrado. Additionally, anthropogenic environments are present, such as roads and access routes, abandoned open-pit quartzite mines, annual and perennial crops, planted pastures, and homogeneous reforestation areas (ICMBio, 2023). The SCNP is located in a region with a typical tropical climate, characterized by two well-defined seasons: a wet season occurring from October to March, and a dry season from April to September. The mean annual rainfall ranges from 1,000 to 1,500 mm, and the average temperature varies between 18°C during the coldest months and 22°C during the warmest months. Elevation ranges from approximately 600 m along the edges of the plateaus to 1,500 m in the mountain ranges and high plateaus (ICMBio, 2023).

2.2 Field data

We employed an adaptation of the distance sampling technique (Burnham et al., 1980), as implemented by Tomas et al. (2021), conducting randomly placed transects in recently burned areas to count and estimate the number of available underground shelter openings in the environment. Transect direction was determined by observers, avoiding areas that were potentially unburned or where dense vegetation impeded the visibility of shelter openings. Transects were established with 10-meter spacing between them to ensure representative sampling of the area and to reduce overlap in detecting the same shelters, thereby maximizing independence among observations. A total of 77 transects were conducted, covering 24,068.67 km.

Distance sampling requires measuring the perpendicular distance between detected target objects and the transect line, as well as the total transect length, to estimate densities based on the detection function. It is assumed that detection probability decreases as distance from the transect line increases (Burnham et al., 1980). Observers worked in pairs, walking transects simultaneously at a constant speed, with one guiding the transect as straight as possible and the other searching for shelter openings and measuring their perpendicular distance to the transect line. All shelters observed within the transect and within a marginal distance of up to 3 meters on either side were recorded, and the opening area of each shelter was measured.

To complement the analyses, temperature measurements were taken during a prescribed burn event. Twenty shelters were selected for monitoring, with temperature recorded at three-time points: before the fire, immediately after fire passage, and five minutes post-fire during thermal stabilization. Temperature measurements inside shelters were performed at approximately 20 cm depth to ensure direct contact with the internal substrate, using an HW600 infrared thermometer with a measurement range of -50ºC to 600ºC, accuracy of ±1.5ºC, resolution of 0.1ºC, response time of 500 ms, and wavelength of 8–14 µm. In addition to shelter temperatures, microhabitat temperatures of the surrounding environment (soil, vegetation, and ash) were also collected. This approach allowed us to evaluate the capacity of shelters to function as thermal refuges against the temperature increases generated by fire.

2.3 Potential for Shelter Use

To infer the potential use of shelter openings by species, we used the list of terrestrial vertebrate species available in the Serra da Canastra National Park management plan (ICMBio, 2025). Each species was classified as having very high, high, medium, or low potential for shelter use (Sup. Table 1), based on three criteria: (i) habit (fossorial, terrestrial, or arboreal); (ii) preferred habitat type (open formations, forest formations, or riparian areas); and (iii) documented records of shelter use, regardless of purpose. Ecological information was obtained from the Sistema de Avaliação do Risco de Extinção da Biodiversidade Brasileira (SALVE - ICMBio), the International Union for Conservation of Nature (IUCN), and The Reptile Database. In addition, species were classified into three body size categories: small (less than 1 kg), medium (between 1 kg and 7 kg), and large (greater than 7 kg), according to the average body mass of the species (Emmons & Feer, 1997; Chiarello, 2000).

Since the sampling transects were conducted in open grasslands, species with greater affinity for these environments were considered more likely to use shelter openings as a fire escape and survival strategy. Information on shelter use refers to any evidence that a species may use such structures, including burrows, tree hollows, or crevices in the ground, rocks, or trees, for protection, nesting, or foraging. Species classified as having very high potential were those with fossorial or terrestrial habits, associated with open environments, and with confirmed records of shelter use. Species with high potential were those with the same habits and preference for open environments, but without documented records of shelter use. Species with medium potential included those with either terrestrial or arboreal habits, associated with forest habitats, but with records of shelter use. Lastly, species with low potential included those with arboreal or aquatic habits, associated with humid and forest habitats, and with no known evidence of shelter use. Species for which available data were insufficient for classification were categorized as indeterminate (Sup. Table 1).

2.4 Data analysis

The sizes of the recorded shelter openings were classified based on the opening area (cm^2) and analyzed using percentiles, allowing categorization according to the variation observed in the data. Shelter openings were grouped into six size classes defined by the 10th, 25th, 50th, 75th, and 90th percentiles: very small (≤ P10), small (P10–P25), medium-low (P25–P50), medium-high (P50–P75), large (P75–P90), and very large (> P90). We used Distance 7.3 software (Thomas et al., 2010) to estimate the density and total number of shelter openings. The percentile-based size classes were treated as strata in the analysis, allowing separate estimates for each group and a combined estimate for the entire study area in SCNP. This approach was adopted to assess whether different parts of the landscape provide shelters in varying proportions.

To model the detection function, which estimates the probability of recording a shelter opening as a function of distance from the transect, we tested different types of mathematical functions, given that shelter detection generally decreases with increasing distance from the transect, reducing the risk of underestimating or overestimating the actual number of shelters. Model selection was based on Akaike's Information Criterion (AIC), which identifies the model that best balances goodness of fit and simplicity. We also prioritized models with the lowest coefficient of variation (CV) to ensure greater precision of estimates. Finally, we visually evaluated the detection curves to confirm that the selected model adequately represented the pattern observed in the field.

To analyze how temperatures varied across different microhabitat types (shelters, vegetation, soil, and ash) over time, we first tested for normality using the Shapiro–Wilk test. As some data samples did not follow a normal distribution, we opted for the non-parametric Friedman test to assess whether significant temperature differences existed among microhabitats (shelters, vegetation, and soil) over time (before the fire, immediately after, and five minutes after fire passage). A second Friedman test was conducted, this time including the ash microhabitat but restricted to post-fire time points, to evaluate whether overall differences existed between groups, even though this test does not indicate between which pairs of groups these differences occur. Therefore, when significant differences were detected, we applied pairwise Wilcoxon post hoc tests to identify which microhabitats differed from each other.

To investigate whether species body mass influences the potential use of shelters as a fire protection strategy, we fitted a generalized linear mixed model (GLMM) with binomial distribution. The response variable was the potential use of shelters, previously classified and recoded as binary: 1 for species with very high or high potential, and 0 for those with medium, low, or indeterminate potential. The main explanatory variable was the species' average body mass, to test whether lighter species are more likely to have high potential for shelter use. Taxonomic order was included as a random effect in the model to account for natural differences among groups such as mammals, reptiles, and amphibians.

In addition to the GLMM, we fitted separate generalized linear models (GLMs), considering body mass, habit type (e.g., terrestrial, arboreal), and taxonomic group individually as explanatory variables. We also tested combinations of these variables, such as body mass in association with the taxonomic group. These models were compared using Akaike's Information Criterion (AIC), which allowed us to identify the model that best-balanced goodness of fit and simplicity.

3. Results

A total of 2,767 shelter openings were detected along the linear transects, with opening areas ranging from 1 cm^2 to over 1,000 cm^2. The mean opening area was 158.6 cm^2, with a standard deviation of 220.3 cm^2, demonstrating substantial variability, mainly due to the presence of larger openings. However, the percentile-based analysis revealed a more informative distribution: the values corresponding to the 10th, 25th, 50th, 75th, and 90th percentiles were 16, 45, 108, 208, and 340 cm^2, respectively. The number of shelter openings in each category was 344, 354, 701, 687, 410, and 271, indicating that most shelters were concentrated between the 25th and 75th percentiles, i.e. at intermediate sizes (Figure 2). These results provide a detailed overview of the availability of underground shelters in the environment.

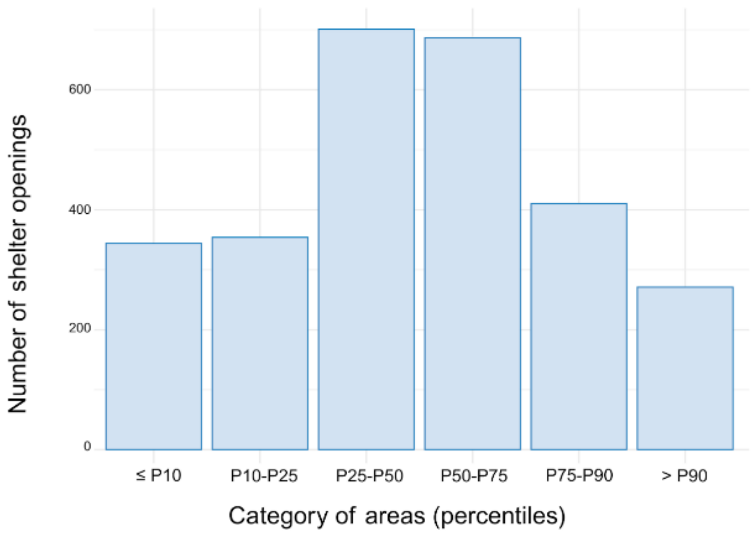


Figure 2: Distribution of recorded shelter opening areas. Categories were defined based on percentiles of the opening area, representing ranges relative to the variability observed in the field.

Analyses conducted in Distance indicated that estimated shelter opening densities varied according to opening area class. The highest density was observed in the P25–P50 class (69.43 openings per hectare), followed by the P50–P75 (54.38 openings per hectare) and ≤P10 (53.09 openings per hectare) classes. The P10–P25 class showed intermediate density (39.65 openings per hectare), while the lowest estimates were recorded for the P75–P90 (32.47 openings per hectare) and >P90 (21.12 openings per hectare) classes. The total estimated number of shelter openings (N) followed the same pattern, with the greatest number estimated in the P25–P50 class, followed by the P50–P75 and ≤P10 classes. Considering all openings combined (n = 2,767), the overall density was 280.70 openings per hectare (CV = 10.60%), with a total estimated number of 3,234 openings (Table 1).

Table 2: Estimates of density (D: shelter openings by hectare) and number of shelter openings (N), their standard errors, coefficient of variation (CV), and confidence interval (CI), by opening area and grouped data. Estimates were obtained through the analysis of distance sampling data in burned areas in Serra da Canastra National Park.

	Paramete r	**Point estimate**	**CV (%)**	**95% CI (in millions)**
<= P10	D	53.09	16.69	38.192 - 73.817
	N	612	16.69	440,00 - 850,00
P10 - P25	D	39.65	20.34	26.571 - 59.155
	N	457	20.34	306,00 - 681,00
P25 - P50	D	69.43	16.43	50.282 - 95.894
	N	800	16.43	579,00 - 1105,00
P50 - P75	D	54.38	14.56	40.850 - 72.383
	N	626	14.56	471,00 - 834,00
P75 - P90	D	32.47	16.26	23.620 - 44.647
	N	374	16.26	272,00 - 514,00
> P90	D	21.12	15.37	15.599 - 28.580
	N	243	15.37	180,00 - 329,00
Pooled	D	280.70	10.60	227.65 - 346.12
	N	3,234	10.60	2622.0 - 3987.0

When examining surface and subsurface temperatures, we observed a marked increase in temperatures across all surface microhabitats immediately after fire passage, with the ash layer showing the highest mean values. In contrast, temperatures inside underground shelters remained stable and low, even immediately after the fire. Residual vegetation and soil showed moderate temperature increases (Figure 3). The Friedman test revealed highly significant differences in temperatures among surface microhabitats (vegetation and soil) at all assessed time points (before the fire, immediately after, and 5 minutes post-fire; $p < 0.000001$). Similarly, when the ash microhabitat was included in analyses for the post-fire time points, differences among the four groups were also highly significant ($p < 0.0000000001$). Pairwise Wilcoxon post hoc tests confirmed that, at all time points, temperatures inside underground shelters differed significantly from those measured in soil, vegetation, and ash (adjusted $p < 0.001$). Furthermore, significant differences were observed between soil and vegetation, as well as between shelters and ash, at the post-fire time points.

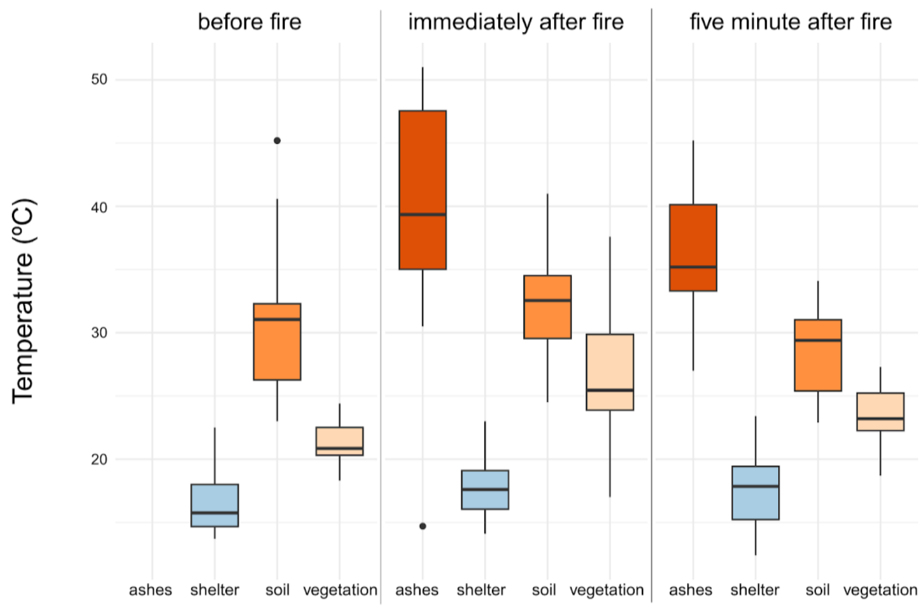


Figure 3: Distribution of mean temperatures (°C) recorded in different microhabitats (underground shelter, vegetation, exposed soil and ash) before the fire, immediately after and five minutes after the fire.

SCNP harbors records of 51 amphibian species, 67 reptiles, 443 birds, and 100 mammals. However, 209 species were analysed, and selected based on their occurrence in terrestrial environments, as these species are more likely to use underground shelters. Of these, 192 species had their potential shelter use determined, while 17 were classified as indeterminate due to insufficient information to meet the established criteria.

Among the 192 classified species, 71 (36.6%) were assigned very high potential, 24 (12.4%) high potential, 46 (23.7%) medium potential, and 51 (26.3%) low potential. Within the very-high-potential group, mammals (29 species), reptiles (25), amphibians (10), and birds

(7) were most represented, with a predominance of small-sized species (49), followed by medium- (18) and large-sized species (4). In the high-potential group, reptiles were most numerous (9 species), followed by amphibians (7), mammals (5), and birds (3), with most species being small (17), medium (5), or large (2). In the medium-potential group, mammals again accounted for the greatest number of species (29), followed by reptiles (8), amphibians (7), and birds (2), with small species predominating (37), followed by medium- (7) and large-sized species (2). Finally, in the low-potential group, mammals represented 21 species, followed by amphibians (16), reptiles (12), and birds (2), with a predominance of small species (38), followed by medium- (10) and large-sized species (3) (Figure 3i and ii; (Sup. Table 2). Moreover, terrestrial and arboreal habits accounted for most of the records for mammals and reptiles, whereas terrestrial habits were predominant among amphibians and birds, and aquatic and fossorial habits were less represented (Figure 3iii).

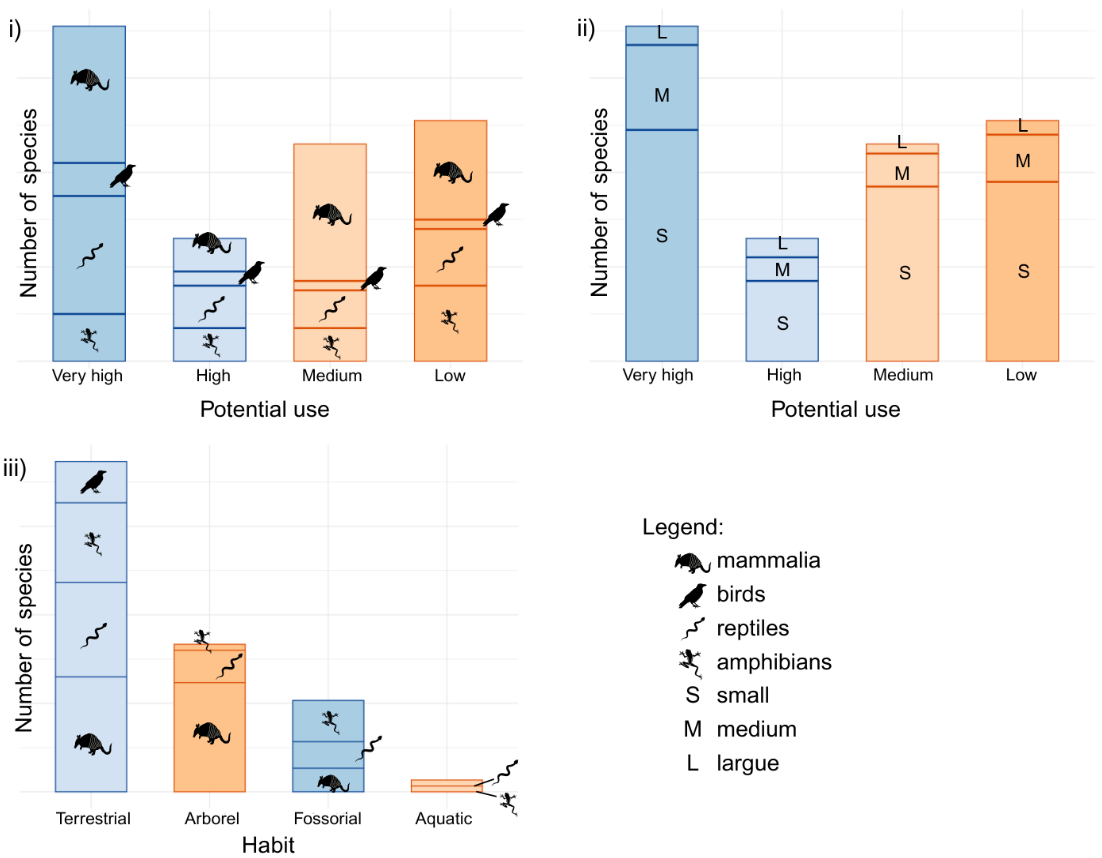


Figure 4: Distribution of potential species for use of shelter openings according to: i) animal group for each registered potential; ii) average body weight category of animals for each registered potential; iii) Habit distribution of species according to animal group.

The single-variable GLMs showed that numerical body mass (AIC = 291.4) was not a strong predictor of shelter-use potential. Including the taxonomic group as a fixed effect slightly improved model fit (AIC = 287.5), though this effect was not significant. The model including habit as a predictor yielded the best fit (AIC = 210.3; deviance = 198.27), suggesting that habit may be the most informative variable for explaining shelter-use potential. The GLMM, which included taxonomic order as a random effect, also did not achieve a good overall fit (AIC = 269.0; deviance = 263.0), with fixed effects not reaching statistical significance (estimate = –0.015, $p = 0.464$). Deviance analysis (Wald chi-square) confirmed the lack of a significant effect of body mass on shelter-use potential ($\chi^2 = 0.537$, df = 1, $p = 0.464$), indicating that other factors, such as habit, may be more important than body size in determining shelter-use patterns.

4. Discussion

To our knowledge, this research represents the first study to estimate the density of underground shelter openings that may offer protection to wildlife during fire events in fire-prone environments, such as the Brazilian Cerrado. The high estimated density of shelter openings in Serra da Canastra National Park (PNSC) suggests that these underground structures play a key role in safeguarding vertebrate fauna across Cerrado grassland ecosystems during fire disturbances, given the satisfactory precision of the estimates.

In this biome, fire-related mortality rates tend to be relatively lower compared to other environments (Costa et al., 2013; Pereira et al., 2025b), which may be attributed to the historical fire regime and the ecological attributes of species, that favor their persistence and promote the selection of evolutionary adaptations to survive in fire-prone landscapes (Jones et al., 2023; Nimmo et al., 2023). Beyond morphological and physiological adaptations that enhance fire survival, there is increasing evidence that animals also develop ecological learning processes related to fire, a phenomenon termed pyro-cognition, that enable them to recognize fire-associated cues and respond with more complex cognitive abilities, such as memory, consequence prediction, and even planning (Jacobs, 2022). Individual learning can improve an organism's responses to new environmental conditions, and when new behaviors are transmitted horizontally to other individuals of the same species or vertically across generations, the entire population may benefit from these fire-adaptive strategies (Sih et al., 2011).

Building upon this context, we formulated our hypothesis that the observed low mortality is associated with the combination of ecological learning and the availability of underground shelter openings. Our results support this hypothesis, suggesting that local fauna may exhibit behaviors and adaptive strategies shaped by the recurrent fire regime in the Cerrado. Moreover, familiarity with the landscape may play a key role in survival during extreme events (Piper, 2011). In familiar environments, individuals can recognize and navigate more efficiently to previously identified refuges, such as underground shelters, when facing imminent threats. This spatial knowledge, coupled with the immobility of these shelters, facilitates their repeated and targeted use as safe refuges. Behavioral ecology research highlights that many vertebrates are capable of forming cognitive maps of their surroundings and utilizing these representations in survival decisions (Shettleworth, 2001; Penndorf & Aplin, 2020). Hence, in fire-prone areas, spatial familiarity may represent an important adaptive advantage for species.

The use of burrows is extensively documented in the scientific literature for both burrowing species and commensals and is associated with a variety of ecological functions, including thermoregulation, predator avoidance, nesting, and sheltering during environmental disturbances (Desbiez & Kluyber, 2013; Di Blanco et al., 2020; Haussmann et al., 2023; Santos et al., 2025). In this context, under imminent threats, such as approaching fire, even individuals that do not typically use these shelters may resort to them as an emergency survival strategy.

Regarding temperature, surface vegetation and soil showed increases. In contrast, underground shelters remained thermally stable, demonstrating that thermal variation can be fundamental for animal survival during and after fire events. These findings underscore the protective value of shelters, not only during active fire but also in the hours immediately afterward, when the external environment can remain inhospitable due to residual heat. Many animals that inhabit areas with strong seasonal thermal fluctuations frequently exhibit physiological and behavioral adaptations to cope with thermal extremes and reduce thermoregulatory costs, allowing them to persist under adverse thermal conditions (McCafferty et al., 2017; Milling et al., 2018; Clifton et al., 2023). For example, in Australia, wombats use their burrows to buffer the thermal stress associated with maintaining body temperature (Morris et al., 2024).

Such shelters typically offer excellent temperature buffering due to soil insulation (Stark et al., 2023), proving especially important for providing thermal refuges when surface temperatures impose high regulatory costs or exceed an organism’s physiological tolerances (Milling et al., 2018). These refuges are generally cooler when ambient conditions aboveground are hotter (Di Blanco et al., 2020), creating more stable microclimates that benefit both the excavating species and other commensals (Richardson & Anderson, 2005).

The presence of fire can be compared to extreme climatic events, imposing lethal environmental conditions, especially for small vertebrates with environmentally dependent thermoregulation, such as lizards and snakes, which are highly sensitive to elevated temperatures unless adequately sheltered with thermal insulation (Costa et al., 2013; de-Carvalho & Citeli, 2022; Pereira et al., 2025a *unpublished results*). Soil temperature during fire decreases rapidly with depth, as mineral soil is an inefficient heat conductor (Enninful & Torvi, 2008; Tangney et al., 2020). In the Cerrado, these thermal variations become negligible below 5 cm depth, and the maximum temperature measured at 7 cm occurs approximately one hour after the fire, not exceeding 25°C (Miranda et al., 1993). These findings reinforce the role of underground shelters as effective thermal barriers, providing protection during and after the passage of fire.

The categorization employed in this study served as an inferential tool, drawing on empirical knowledge and evidence related to species' ecology and predator-defense mechanisms to identify those that may use this strategy for survival. For instance, in savanna ecosystems, one key anti-predatory strategy adopted by small rodents is seeking refuge within vegetation or burrows. The abundant cavities created by armadillos and other mammals, such as *Clyomys bishopi*, can offer shelter from many terrestrial and aerial predators (Bueno & Motta-Junior, 2015).

We believe that fossorial species are more adept at locating and utilizing underground shelters when alerted, and the GLM analyses indicated that species' habits are the most important predictor for shelter use. In the central Brazilian Cerrado, Costa et al. (2013) documented both fossorial and terrestrial lizards sheltering in burrows and termite mounds during fires, characterizing these burrows as primary refuges for lizards against fire, even when other types of shelters were available. Moreover, additional research has emphasized that herpetofauna may employ a variety of mechanisms to survive, including fleeing and burrowing (Certini et al., 2021). Turtles and amphibians also bury themselves to survive fire events (Driscoll & Henderson, 2008).

Although species weight was not a significant predictor of shelter use in either the GLM or GLMM analyses, smaller-bodied species were predominant in the categories with the highest shelter-use potential, suggesting that body size may influence the capacity to utilize underground refuges, corroborating Batista et al. (2023). Small ground-dwelling mammals tend to flee or move through tunnels as fire approaches (Dawson et al., 2019). In the Brazilian Cerrado, the didelphid *Gracilinanus agilis* was not directly affected by fire, suggesting that its small body size and scansorial habits enable this species to escape the fire by seeking refuge in tree hollows and underground burrows (Rossi & Leiner, 2023). In general, small rodents, reptiles, and amphibians have been observed within armadillo burrows (Santos et al., 2025). Nevertheless, several medium and large bodied mammals, including *Dicotyles tajacu, Tayassu pecari*, and *Myrmecophaga tridactyla,* have also been recorded using armadillo burrows in the Pantanal (Santos et al., 2025). Furthermore, different species may share the same shelter under imminent threat, as exemplified in the Pantanal where one *Leopardus pardalis* and one *Panthera onca* were documented occupying the same artificial refuge during a wildfire (Pereira et al., 2025a *unpublished results*).

Underground shelters are also essential to ensure that individuals surviving in a given area are responsible for the maintenance and recolonization of fire-affected sites (Banks et al., 2011; Hale et al., 2022). This further suggests that the persistence of populations after fire events depends strongly on in situ survival, reinforcing the role of underground refuges in ensuring long-term population viability post-fire (Watchorn et al., 2024). Hence, stable and effective refuges not only guarantee survival during the event itself but also support the ecological recovery of the local community, further emphasizing the relevance of conserving microhabitats that serve as safe zones (Robinson et al., 2013).

Armadillos are well-known ecosystem engineers (Rodrigues et al., 2020), with a single species capable of creating networks of burrows that benefit many other species. In the PNSC, six armadillo species, *Cabassous tatouay*, *C. unicinctus*, *Dasypus novemcinctus*, *D. septemcinctus*, *Euphractus sexcinctus*, and *Priodontes maximus*, create microenvironments through their burrows that allow animals to shelter from extreme environmental conditions (Di Blanco et al., 2020; Desbiez et al., 2021). Knapp et al. (2018) emphasized the importance of ecosystem engineers in fire-prone landscapes. In Australia, 47 vertebrate species have been recorded using wombat burrows as shelter during wildfires (Linley et al., 2024). In the USA, vertebrate use of *Gopherus polyphemus* burrows was eight times higher at prescribed burn sites than at unburned sites (Knapp et al., 2018). Furthermore, the use of burrows by commensal species during disturbance events supports that facilitative interactions among species become more important under adverse ecological conditions (Lowney & Thomson, 2021).

Based on shelter opening dimensions and animals' body size, we can infer that smaller shelter openings are likely constructed by small animals, while larger shelter openings are built by larger animals. This is consistent with the tendency for larger species to construct larger burrows in the environment (Woolnough & Steele, 2001). However, Van Vuren & Ordeñana (2012) found that some species excavate burrows with volumes disproportionate to their body size, often highly social species that share their burrows with other individuals.

For larger shelters, we infer that in addition to having space to house small animals, they are also compatible with medium and large animals. For example, *Priodontes maximus* (the giant armadillo) is a large burrowing species weighing up to 60 kg. The mean dimensions of its burrow entrances are 36 cm in length (±7 cm) and 43 cm in width (±9 cm), which can also be used by various medium- and large-sized vertebrates (Silveira et al., 2009; Ceresoli & Fernandez-Duque, 2012; Desbiez & Kluyber, 2013; Desbiez et al., 2019). Fragoso et al. (2024) documented for the first time a *Panthera onca* (jaguar), the largest felid in the Americas (IUCN, 2022), utilizing a giant armadillo burrow, potentially as a thermal refuge. Furthermore, Yan et al. (2025) showed that giant armadillo burrows are a valuable shelter resource for *Tamandua tetradactyla* (the collared anteater), suggesting that its conservation depends on preserving the giant armadillo, a species assessed as vulnerable.

Finally, it is important to emphasize that although fire is a natural component of many ecosystems, such as the Cerrado, it can represent a potentially lethal event for wildlife (Pereira et al., 2025b). Species that evolved in fire-prone environments are adapted to a specific fire regime, including its frequency, intensity, severity, extent, and seasonality, but this does not imply that they can survive any fire event (Keeley et al., 2011; Pausas & Parr, 2018). Thus, we highlight that the persistence of wildlife in burned areas depends not only on direct adaptations to fire but also on the availability of effective refuges that enable animals to endure the fire front and the post-fire period, when food resources and shelters are drastically reduced. Moreover, we underscore the significant impacts that ecosystem engineers have on the physical structure of their habitats and on the organisms that inhabit them.

5. Conclusions and Recommendations

We demonstrated that the physical structure of the Cerrado grassland environment provides a functional network of thermally stable underground shelters that are readily accessible to wildlife. This feature may be one of the key factors explaining the resilience of animal communities in fire-prone areas, such as those observed in Serra da Canastra National Park. Our findings contribute to a deeper understanding of the mechanisms underlying wildlife persistence under recurrent fire regimes. Specifically, maintaining soil structure through the protection of ecological processes, such as burrowing by ecosystem engineers, may be crucial for biodiversity conservation in open Cerrado landscapes. Future studies could build upon this work by surveying burrow entrances before and after fire to determine whether animals only use existing burrows or excavate new ones during fire events, and by employing environmental

DNA analyses to identify which species use burrows of different sizes before, during and after burns.

Taken together with the absence of observed animal mortality, these results indicate that properly timed prescribed burns in the Cerrado biome, using appropriate ignition patterns, can support vertebrate conservation. Nevertheless, further research is needed to understand the effects of fire on species' home ranges and movement behavior to optimize the size of burned patches, even if this requires greater field effort to implement smaller, more targeted burns.

Acknowledgements

The authors acknowledge the firefighter that support the field and the financial support provided by the Coordination for the Improvement of Higher Education Personnel (CAPES - financing code 001) and National Council for Scientific and Technological Development (CNPq) for the scholarship granted to A. R. Pereira (this article is a part of her Master's research) and through the funding of the project 'Efeitos do fogo sobre a abundância e diversidade de vertebrados do Parque Nacional da Serra da Canastra' CNPq/MCTI/FNDCT No. 18/2021, process nº 406473/2021-8. We would also like to thank the Specialized Center for Integrated Fire Management of the Chico Mendes Institute for Biodiversity Conservation (CEMIF/ICMBio) and the Federal University of Viçosa (UFV) and the Postgraduate Program in Forestry Science (PPGCF - UFV) for financing the field work. Finally, we would like to thank the members of the Forest Fires and Nature Conservation Laboratory (DEF-UFV) and to all the people who contributed to the collection of field data.

References

Álvarez-Ruiz, L., Belliure, J., Pausas, J.G., 2021. Fire-driven behavioral response to smoke in a Mediterranean lizard. Behavioral Ecology, 32(4), 662-667. https://doi.org/10.1093/beheco/arab010

Banks, S.C., Dujardin, M., McBurney, L., Blair, D., Barker, M., Lindenmayer, D.B., 2011. Starting points for small mammal population recovery after wildfire: Recolonisation or residual populations? Oikos, 120, 26–37. https://doi.org/10.1111/j.1600-0706.2010.18765.x

Batista, E.K.L., Figueira, J.E.C., Solar, R.R., de Azevedo, C.S., Beirão, M.V., Berlinck, C.N., ... Fernandes, G.W., 2023. In case of fire, escape or die: a trait-based approach for identifying animal species threatened by fire. Fire, 6(6), 242. https://doi.org/10.3390/fire6060242

Batista, E.K.L., Russell-Smith, J., França, H., Figueira, J.E.C., 2018. An evaluation of contemporary savanna fire regimes in the Canastra National Park, Brazil: Outcomes of fire suppression policies. Journal of Environmental Management, 205, 40-49. https://doi.org/10.1016/j.jenvman.2017.09.053

Bueno, A.D.A., Motta-Junior, J.C., 2015. Behavioural and morphological strategies by small savannah rodents to avoid predation. Mammalian Biology, 80, 401-408. https://doi.org/10.1016/j.mambio.2015.05.005

Burnham, K.P., Anderson, D.R., Laake, J.L., 1980. Estimation of density from line transect sampling of biological populations. Wildlife monographs, (72), 3-202. http://www.jstor.org/stable/3830641

Ceresoli, N., Fernandez-Duque, E., 2012. Size and orientation of giant armadillo burrow entrances (*Priodontes maximus*) in western Formosa province, Argentina. Edentata, 13(1), 66-68. https://doi.org/10.5537/020.013.0109
Certini, G., Moya, D., Lucas-Borja, M.E., Mastrolonardo, G., 2021. The impact of fire on soil-dwelling biota: A review. Forest Ecology and Management, 488, 118989. https://doi.org/10.1016/j.foreco.2021.118989

Chiarello, A.G., 2000. Density and population size of mammals in remnants of Brazilian Atlantic Forest. Conserv. Biol. 14 (6), 1649–1657. https://doi.org/10.1111/j.1523-1739.2000.99071.x

Clifton, I.T., Duffy, M.R., Hudson, S.B., Robinson, C.D., Virgin, E.E., French, S.S., ... Refsnider, J.M., 2023. Compensation for exposure to increased environmental temperatures is costly in a montane, desert lizard. Journal of Arid Environments, 219, 105079. https://doi.org/10.1016/j.jaridenv.2023.105079

Costa, B.M., Pantoja, D.L., Vianna, M.C.M., Colli, G.R., 2013. Direct and short-term effects of fire on lizard assemblages from a Neotropical savanna hotspot. Journal of Herpetology, 47(3), 502-510. https://doi.org/10.1670/12-043

Dawson, S.J., Broussard, L., Adams, P.J., Moseby, K.E., Waddington, K.I., Kobryn, H.T., ... Fleming, P.A., 2019. An outback oasis: the ecological importance of bilby burrows. Journal of Zoology, 308(3), 149-163. https://doi.org/10.1111/jzo.12663

de-Carvalho, M., & Citeli, N. (2022). Welcome to the Hotel Termitaria: A Safe Place for Snakes. Wilderness & Environmental Medicine, 33(2), 259-260. https://doi.org/10.1016/j.wem.2022.02.00

Desbiez, A.L.J., Massocato, G.F., Kluyber, D., 2019. Insights into giant armadillo (Priodontes maximus Kerr, 1792) reproduction. Mammalia, 84(3), 283-293. https://doi.org/10.1515/mammalia-2019-0018

Desbiez, A.L.J., Kluyber, D., 2013. The role of giant armadillos (*Priodontes maximus*) as physical ecosystem engineers. Biotropica, 45(5), 537-540. https://doi.org/10.1111/btp.12052

Desbiez, A.L.J., Kluyber, D., Massocato, G.F., Attias, N., 2021. Methods for the characterization of activity patterns in elusive species: the giant armadillo in the Brazilian pantanal. Journal of Zoology, 315, 301–312. https://doi.org/10.1111/jzo.12921

Di Blanco, Y.E., Desbiez, A.L., Di Francescantonio, D., Di Bitetti, M. S., 2020. Excavations of giant armadillos alter environmental conditions and provide new resources for a range of animals. Journal of Zoology, 311(4), 227-238. https://doi.org/10.1111/jzo.12782

Doherty, T.S., Geary, W.L., Jolly, C.J., Macdonald, K.J., Miritis, V., Watchorn, D.J., Dickman, C.R., 2022. Fire as a driver and mediator of predator–prey interactions. Biol. Rev. 97 (4), 1539–1558. https://doi.org/10.1111/brv.12853

Driscoll, D.A., Henderson, M.K., 2008. How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. Biological Conservation, 141(2), 460-471. https://doi.org/10.1016/j.biocon.2007.10.016

Durigan, G., 2020. Zero-fire: Not possible nor desirable in the Cerrado of Brazil. Flora, 268, 151612. https://doi.org/10.1016/j.flora.2020.151612

Durigan, G., Ratter, J.A., 2016. The need for a consistent fire policy for Cerrado conservation. Journal of Applied Ecology, 53(1), 11-15. https://doi.org/10.1111/1365-2664.12559

Emmons, L.H., Feer, F., 1997. Neotropical Rainforest Mammals: A Field Guide. University of Chicago Press, Chicago and London.

Engstrom, R.T., 2010. First-order fire effects on animals: review and recommendations. Fire Ecology, 6, 115-130. https://doi.org/10.4996/fireecology.0601115

Enninful, E.K., Torvi, D.A., 2008. A variable property heat transfer model for predicting soil temperature profiles during simulated wildland fire conditions. International Journal of Wildland Fire, 17(2), 205-213. https://doi.org/10.1071/WF07002

Fragoso, C.E., Nascimento, T.E., Desbiez, A.L., 2024. Underground jaguars: first record of a jaguar (*Panthera onca*) using a giant armadillo (*Priodontes maximus*) burrow. Notas sobre Mamíferos Sudamericanos, 6(1). https://doi.org/10.31687/SaremNMS24.08.5

Franke, J., Barradas, A.C.S., Borges, K.M.R., Hoffmann, A.A., Orozco Filho, J.C., Ramos, R.M., ... Roman-Cuesta, R.M., 2024. Prescribed burning and integrated fire management in the Brazilian Cerrado: demonstrated impacts and scale-up potential for emission abatement. Environmental Research Letters, 19(3), 034020. https://doi.org/10.1088/1748-9326/ad2820

Hale, S., Mendoza, L., Yeatman, T., Cooke, R., Doherty, T., Nimmo, D., White, J.G., 2022. Evidence that post-fire recovery of small mammals occurs primarily via in situ survival. Diversity and Distributions, 28(3), 404-416. https://doi.org/10.1111/ddi.13283

Haussmann, N.S., Blomsterberg-Reyneke, S.E., le Roux, P.C., McIntyre, T., Bennett, N.C., 2023. Multi-Species Visits to an Aardvark Burrow–Whose Turn Is It Next?. African Journal of Wildlife Research, 53(1). https://doi.org/10.3957/056.053.0006

He, T., Lamont, B.B., Pausas, J.G., 2019. Fire as a key driver of Earth's biodiversity. Biological Reviews, 94(6), 1983–2010. https://doi.org/10.1111/brv.12544

ICMBio - Instituto Chico Mendes de Conservação da Biodiversidade, 2023. Plano de manejo: Parque Nacional da Serra da Canastra. MMA/ICMBio. 64p.

ICMBio - Instituto Chico Mendes de Conservação da Biodiversidade, 2025. Espécies Fauna Serra da Canastra. https://www.gov.br/icmbio/pt-br/assuntos/biodiversidade/unidade-de-conservacao/unidades-de-biomas/cerrado/lista-de-ucs/parna-da-serra-da-canastra/arquivos/especies-fauna-serra-da-canastra%2025.04.2025.pdf/view (accessed 28 April 2025).

Jacobs, I., 2022. Animal response to fire, in: Vonk, J., Shackelford, T.K. (Eds), Encyclopedia of animal cognition and behavior. Cham: Springer International Publishing, pp. 314-317. https://doi.org/10.1007/978-3-319-55065-7_2095

Jolly, W.M., Cochrane, M.A., Freeborn, P.H., Holden, Z.A., Brown, T.J., Williamson, G.J., Bowman, D.M., 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. Nature communications, 6(1), 7537. https://doi.org/10.1038/ncomms8537

Jolly, C.J., Dickman, C.R., Doherty, T.S., van Eeden, L.M., Geary, W.L., Legge, S.M., …, Nimmo, D.G., 2022. Animal mortality during fire. Global Change Biology, 28(6), 2053-2065. https://doi.org/10.1111/gcb.16044

Jones, G.M., Goldberg, J.F., Wilcox, T.M., Buckley, L.B., Parr, C.L., Linck, E.B., ... Schwartz, M.K., 2023. Fire-driven animal evolution in the Pyrocene. Trends in Ecology & Evolution, 38(11), 1072-1084. https://doi.org/10.1016/j.tree.2023.06.003

Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J., Bradstock, R.A., 2011. Fire as an evolutionary pressure shaping plant traits. Trends in plant science, 16(8), 406-411. https://doi.org/10.1016/j.tplants.2011.04.002

Kelly, L.T., Giljohann, K.M., Duane, A., Aquilué, N., Archibald, S., Batllori, E., ... Brotons, L., 2020. Fire and biodiversity in the Anthropocene. Science, 370(6519), eabb0355. https://doi.org/10.1126/science.abb03

Knapp, D.D., Howze, J.M., Murphy, C.M., Dziadzio, M.C., Smith, L.L., 2018. Prescribed fire affects diurnal vertebrate use of gopher tortoise (*Gopherus polyphemus*) burrows in a longleaf pine (*Pinus palustris*) forest. Herpetological Conservation and Biology, 13(3), 551-557.

Levis, C., Flores, B.M., Campos-Silva, J.V., Peroni, N., Staal, A., Padgurschi, M.C., ... Clement, C.R., 2024. Contributions of human cultures to biodiversity and ecosystem conservation. Nature Ecology & Evolution, 8(5), 866-879. https://doi.org/10.1038/s41559-024-02356-1

Linley, G.D., Geary, W.L., Jolly, C.J., Spencer, E.E., Ashman, K.R., Michael, D.R., Westaway, D.M., Nimmo, D.G., 2024. Wombat burrows are hotspots for small vertebrates in a landscape subject to gigafire. Journal of Mammalogy, 105, 752–764. https://doi.org/10.1093/jmammal/gyae034

Lowney, A.M., Thomson, R.L., 2021. Ecological engineering across a temporal gradient: sociable weaver colonies create year-round animal biodiversity hotspots. The Journal of Animal Ecology, 90(10), 2362–2376. https://doi.org/10.1111/1365-2656.13544

Magioli, M., Lima, L.H.A., Villela, P.M.S., Sampaio, R., Bonjorne, L., Ribeiro, R.L.A., …, Berlinck, C.N., 2024. Forest type modulates mammalian responses to megafires. Scientific reports, 14(1), 13538. https://doi.org/10.1038/s41598-024-64460-3

Martin, R. E., & Sapsis, D. B. (1992). Fires as agents of biodiversity: pyrodiversity promotes biodiversity. *In:* Proceedings of the conference on biodiversity of northwest California ecosystems. Cooperative Extension, University of California, Berkeley (pp. 150-157).

McCafferty, D.J., Pandraud, G., Gilles, J., Fabra-Puchol, M., Henry, P.Y., 2017. Animal thermoregulation: a review of insulation, physiology and behaviour relevant to temperature control in buildings. Bioinspiration & biomimetics, 13(1), 011001. https://doi.org/10.1088/1748-3190/aa9a12

Mendyk, R.W., Weisse, A., Fullerton, W., 2020. A wake-up call for sleepy lizards: The olfactory-driven response of *Tiliqua rugosa* (Reptilia: Squamata: Sauria) to smoke and its implications for fire avoidance behavior. Journal of Ethology, 38(2), 161–166. https://doi.org/10.1007/s10164-019-00628-z

Milling, C.R., Rachlow, J.L., Chappell, M.A., Camp, M.J., Johnson, T.R., Shipley, L.A., ... Forbey, J.S., 2018. Seasonal temperature acclimatization in a semi-fossorial mammal and the role of burrows as thermal refuges. PeerJ, 6, e4511. https://doi.org/10.7717/peerj.4511

Miranda, A.C., Miranda, H.S., Dias, I.D.F.O., de Souza Dias, B.F., 1993. Soil and air temperatures during prescribed cerated fires in Central Brazil. Journal of tropical ecology, 9(3), 313-320. https://doi.org/10.1017/S0266467400007367

Morris, S.D., Johnson, C.N., Brook, B.W., Kearney, M.R., 2024. Seasonal and depth-dependent thermoregulatory benefits of burrows for wombats–The largest burrowing marsupials. Journal of Thermal Biology, 125, 103961. https://doi.org/10.1016/j.jtherbio.2024.103961

Moura, L.C., Scariot, A.O., Schmidt, I.B., Beatty, R., Russell-Smith, J., 2019. The legacy of colonial fire management policies on traditional livelihoods and ecological sustainability in savannas: Impacts, consequences, new directions. Journal of Environmental Management, 232, 600-606. https://doi.org/10.1016/j.jenvman.2018.11.057

Nimmo, D.G., Jolly, C.J., Carthey, A.J., 2023. Expanding the scope of fire-driven animal evolution. Trends in Ecology & Evolution, 38(12), 1115-1116. https://doi.org/10.1016/j.tree.2023.09.005

Nimmo, D.G., Carthey, A.J., Jolly, C.J., Blumstein, D.T., 2021. Welcome to the Pyrocene: Animal survival in the age of megafire. Global Change Biology, 27(22), 5684-5693. https://doi.org/10.1111/gcb.15834

Novato, T.D.S., Albuquerque, U.P., Campos, J.L.A., Soldati, G.T., 2025. Assessment of demographic sustainability of *Comanthera elegans* under traditional management in the Brazilian savanna. Conservation Biology, 39(3), e70028. https://doi.org/10.1111/cobi.70028

Nowack, J., Delesalle, M., Stawski, C., Geiser, F., 2016. Can hibernators sense and evade fires? Olfactory acuity and locomotor performance during deep torpor. The Science of Nature, 103(9), 1-7. https://doi.org/10.1007/s00114-016-1396-6

Pausas, J.G., Parr, C.L., 2018. Towards an understanding of the evolutionary role of fire in animals. Evolutionary Ecology, 32(2), 113-125. https://doi.org/10.1007/s10682-018-9927-6

Penndorf, J., Aplin, L., 2020. Environmental and life history factors, but not age, influence social learning about food: a meta-analysis. Animal Behaviour, 167, 161-176. https://doi.org/10.1016/j.anbehav.2020.07.001

Pereira, A.R., Torres, F.T.P., Berlinck, C.N., 2025. Hidden Flames: Uncovering the Indirect Impact of Fire on Brazilian Wildlife. (Manuscript submitted at *Journal for Nature Conservation*). Department of Forest Engineering, Federal University of Viçosa, Brazil.

Pereira, A.R., Torres, F.T.P., Berlinck, C.N., 2025. Ecological implications of the direct effects of fire on neotropical vertebrates. Science of The Total Environment, 979, 179437. https://doi.org/10.1016/j.scitotenv.2025.179437

Piper, W. H., 2011. Making habitat selection more "familiar": a review. Behavioral Ecology and Sociobiology, 65, 1329-1351. https://doi.org/10.1007/s00265-011-1195-1

Pivello, V.R., Vieira, I., Christianini, A.V., Ribeiro, D.B., da Silva Menezes, L., Berlinck, C.N., ... Overbeck, G.E., 2021. Understanding Brazil's catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. Perspectives in Ecology and Conservation, 19(3), 233-255. https://doi.org/10.1016/j.pecon.2021.06.005

Pocknee, C.A., Legge, S.M., McDonald, J., Fisher, D.O., 2023. Modeling mammal response to fire based on species' traits. Conservation Biology, 37(4), e14062. https://doi.org/10.1111/cobi.14062

Richardson, P.R., Anderson, M.D., 2005. The physical and thermal characteristics of aardwolf dens. South African Journal of Wildlife Research, 35(2), 147-153.

Robinson, N.M., Leonard, S.W., Ritchie, E.G., Bassett, M., Chia, E.K., Buckingham, S., …, Clarke, M.F., 2013. Refuges for fauna in fire-prone landscapes: their ecological function and importance. Journal of Applied Ecology, 50(6), 1321-1329. https://doi.org/10.1111/1365-2664.12153

Rodrigues, T.F., Mantellatto, A.M., Superina, M., Chiarello, A. G., 2020. Ecosystem services provided by armadillos. Biological Reviews, 95(1), 1-21. https://doi.org/10.1111/brv.12551

Rossi, R.C., Leiner, N.O., 2023. Effects of severe fires on the survival and body condition of Gracilinanus agilis in a Cerrado remnant. Mammalian Biology, 103(2), 205-214. https://doi.org/10.1007/s42991-022-00340-5

Santos, F.M., Sano, N.Y., de Assis, W.O., Nascimento, L.F., de Oliveira, J., Fonseca, C., ... de Oliveira Porfirio, G.E., 2025. Armadillo burrows: a meeting point for biodiversity in the Pantanal Wetland. Mammalian Biology, 105, 379–386. https://doi.org/10.1007/s42991-024-00466-8

Schmidt, I.B., Moura, L.C., Ferreira, M.C., Eloy, L., Sampaio, A.B., Dias, P.A., Berlinck, C.N., 2018. Fire management in the Brazilian savanna: First steps and the way forward. Journal of Applied Ecology, 55(5), 2094-2101. https://doi.org/10.1111/1365-2664.13118

Semedo, T.B.F. et al. (2022). Escaping the flames. *In*: Pantanal Science. 7(1), 19-2. ISSN 2357-9056.

Semedo, T.B.F., Libardi, G.S., Strüssmann, C., Berlinck, C.N., Tomas, W.M., Garbino, G.S.T., 2022. Discovery of underground shelters occupied by the Chacoan Marsh Rat after massive wildfires in Pantanal, Brazil. Therya Notes, 3, 30-35. https://doi.org/10.12933/therya_notes-22-65

Shettleworth, S.J., 2001. Animal cognition and animal behaviour. Animal behaviour, 61(2), 277-286. https://doi.org/10.1006/anbe.2000.1606

Sih, A., Ferrari, M. C., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary applications, 4(2), 367-387. https://doi.org/10.1111/j.1752-4571.2010.00166.x

Silveira, L., de Almeida Jácomo, A.T., Furtado, M.M., Torres, N.M., Sollmann, R., Vynne, C., 2009. Ecology of the giant armadillo (*Priodontes maximus*) in the grasslands of central Brazil. Edentata, 2009(10), 25-34. https://doi.org/10.1896/020.010.0112

Souza, C.V., Lourenço, Á., Vieira, E.M., 2023. Species-specific responses of medium and large mammals to fire regime attributes in a fire-prone neotropical savanna. Fire, 6(3), 110. https://doi.org/10.3390/fire6030110

Stark, G., Ma, L., Zeng, Z.G., Du, W.G., Levy, O., 2023. Cool shade and not-so-cool shade: How habitat loss may accelerate thermal stress under current and future climate. Global Change Biology, 29(22), 6201-6216. https://doi.org/10.1111/gcb.16802

Steel, Z.L., Miller, J.E., Ponisio, L.C., Tingley, M.W., Wilkin, K., Blakey, R., ... Jones, G., 2023. A roadmap for pyrodiversity science. Journal of Biogeography, 51(2), 280-293. https://doi.org/10.1111/jbi.14745

Tangney, R., Merritt, D.J., Callow, J.N., Fontaine, J.B., Miller, B.P., 2020. Seed traits determine species' responses to fire under varying soil heating scenarios. Functional Ecology, 34(9), 1967-1978. https://doi.org/10.1111/1365-2435.13623

Tomas, W.M., Berlinck, C.N., Chiaravalloti, R.M., Faggioni, G.P., Strüssmann, C., Libonati, R., ... Morato, R., 2021. Distance sampling surveys reveal 17 million vertebrates directly killed by the 2020's wildfires in the Pantanal, Brazil. Scientific Reports, 11(1), 23547. https://doi.org/10.1038/s41598-021-02844-5

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., ... Burnham, K.P., 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology, 47(1), 5-14. https://doi.org/10.1111/j.1365-2664.2009.01737.x

Van Vuren, D. H., & Ordeñana, M. A. (2012). Factors influencing burrow length and depth of ground-dwelling squirrels. Journal of Mammalogy, 93(5), 1240-1246. https://doi.org/10.1644/12-MAMM-A-049.1

Watchorn, D.J., Dickman, C.R., Greenville, A., Wilson, B.A., Garkaklis, M.J., Driscoll, D.A., ... Doherty, T.S., 2024. Artificial refuges provide post-fire habitat for small vertebrates. Biological Conservation, 291, 110501. https://doi.org/10.1016/j.biocon.2024.110501

Woolnough, A.P., Steele, V.R., 2001. The palaeoecology of the Vombatidae: did giant wombats burrow?. Mammal Review, 31(1), 33-45. https://doi.org/10.1046/j.1365-2907.2001.00077.x

Wu, C., Venevsky, S., Sitch, S., Mercado, L.M., Huntingford, C., Staver, A.C., 2021. Historical and future global burned area with changing climate and human demography. One Earth, 4(4), 517–530. https://doi.org/10.1016/j.oneear.2021.03.002

Yan, M., Bertassoni, A., Massocato, G.F., Desbiez, A.L.J., 2025. ‘Knocking’on armadillo's door: Uncovering the use of an ecosystem Engineer's burrow by the lesser anteater. Journal of Zoology. https://doi.org/10.1111/jzo.70006

Supplementary material

Table 1: Criteria used to classify species according to their potential to use shelters as refuge from fire. The classification was based on species’ habits, preferred habitat types, and the existence of documented records of shelter use and purpose of use.

Potencial	**Main criteria**
Very High	Fossorial or terrestrial habit + open habitat + presence of records of shelter use.
High	Fossorial or terrestrial habit + open habitat + no records of shelter use.
Medium	Terrestrial habit + forest habitat + presence of records of shelter use.
Low	Arboreal or aquatic habit + humid or forest habitats + no records of shelter use.
Indeterminate	Insufficient ecological information for reliable classification.

Table 2:

Grup	**Specie**	**Potencial**
Mammals	*Caluromys philander*	Low
Mammals	*Didelphis albiventris*	Very high
Mammals	*Gracilinanus agilis*	Low
Mammals	*Gracilinanus microtarsus*	Medium
Mammals	*Lutreolina crassicaudata*	Very high
Mammals	*Marmosops incanus*	Low
Mammals	*Metachirus nudicaudatus*	Medium
Mammals	*Monodelphis americana*	Medium
Mammals	*Monodelphis dimidiata*	Medium
Mammals	*Monodelphis domestica*	Medium
Mammals	*Cabassous tatouay*	Very high
Mammals	*Cabassous unicinctus*	Very high
Mammals	*Dasypus novemcinctus*	Very high
Mammals	*Dasypus septemcinctus*	Very high
Mammals	*Euphractus sexcinctus*	Very high
Mammals	*Priodontes maximus*	Very high
Mammals	*Myrmecophaga tridactyla*	Very high
Mammals	*Tamandua tetradactyla*	Medium
Mammals	*Anoura caudifer*	Medium
Mammals	*Anoura geoffroyi*	Medium
Mammals	*Artibeus fimbriatus*	Low
Mammals	*Artibeus lituratus*	Low
Mammals	*Artibeus planirostris*	Low
Mammals	*Carollia perspicillata*	Indeterminate
Mammals	*Desmodus rotundus*	Medium
Mammals	*Glossophaga soricina*	Low
Mammals	*Micronycteris megalotis*	Medium
Mammals	*Micronycteris minuta*	Medium
Mammals	*Phyllostomus hastatus*	Medium
Mammals	*Platyrrhinus lineatus*	Low
Mammals	*Sturnira lilium*	Low
Mammals	*Dasypterus ega*	Indeterminate
Mammals	*Myotis nigricans*	Medium
Mammals	*Histiotus montanus*	Medium
Mammals	*Eptesicus furinalis*	Medium
Mammals	*Nyctinomops laticaudatus*	Medium
Mammals	*Callithrix jacchus*	Low
Mammals	*Callithrix penicillata*	Low
Mammals	*Alouatta caraya*	Low
Mammals	*Alouatta guariba*	Low
Mammals	*Sapajus apella*	Low
Mammals	*Callicebus personatus*	Low

Mammals	*Cerdocyon thous*	Very high
Mammals	*Chrysocyon brachyurus*	High
Mammals	*Lycalopex vetulus*	Very high
Mammals	*Herpailurus yagouaroundi*	Low
Mammals	*Leopardus tigrinus*	High
Mammals	*Leopardus wiedii*	Low
Mammals	*Leopardus colocolo*	High
Mammals	*Puma concolor*	Low
Mammals	*Lontra longicaudis*	Indeterminate
Mammals	*Eira barbara*	Medium
Mammals	*Galictis cuja*	High
Mammals	*Nasua nasua*	Medium
Mammals	*Procyon cancrivorus*	Medium
Mammals	*Dicotyles tajacu*	Very high
Mammals	*Tayassu pecari*	Very high
Mammals	*Mazama americana*	Low
Mammals	*Subulo gouazoubira*	Indeterminate
Mammals	*Ozotoceros bezoarticus*	High
Mammals	*Akodon lindberghi*	Very high
Mammals	*Akodon montensis*	Medium
Mammals	*Oligoryzomys fornesi*	Very high
Mammals	*Calomys callosus*	Very high
Mammals	*Calomys laucha*	Very high
Mammals	*Calomys tener*	Very high
Mammals	*Cerradomys subflavus*	Very high
Mammals	*Euryoryzomys lamia*	Medium
Mammals	*Necromys lasiurus*	Very high
Mammals	*Nectomys squamipes*	Indeterminate
Mammals	*Oligoryzomys microtis*	Medium
Mammals	*Oligoryzomys moojeni*	Very high
Mammals	*Oligoryzomys nigripes*	Very high
Mammals	*Oxymycterus delator*	Very high
Mammals	*Oxymycterus roberti*	Very high
Mammals	*Oxymycterus dasytrichus*	Medium
Mammals	*Rhipidomys mastacalis*	Low
Mammals	*Thalpomys cerradensis*	Very high
Mammals	*Thalpomys lasiotis*	Very high
Mammals	*Hylaeamys megacephalus*	Medium
Mammals	*Cuniculus paca*	Medium
Mammals	*Coendou prehensilis*	Medium
Mammals	*Coendou insidiosus*	Medium
Mammals	*Cavia aperea*	Very high
Mammals	*Hydrochoerus hydrochaeris*	Low
Mammals	*Dasyprocta leporina*	Medium
Mammals	*Clyomys laticeps*	Very high

Mammals	*Thrichomys apereoides*	Very high
Mammals	*Sylvilagus brasiliensis*	Medium
Reptile	*Boa constrictor*	High
Reptile	*Epicrates crassus*	Low
Reptile	*Apostolepis assimilis*	Low
Reptile	*Chironius flavolineatus*	Low
Reptile	*Chironius quadricarinatus*	High
Reptile	*Erythrolamprus aesculapii*	Medium
Reptile	*Erythrolamprus almadensis*	Medium
Reptile	*Erythrolamprus jaegeri*	Very high
Reptile	*Erythrolamprus poecilogyrus*	Very high
Reptile	*Erythrolamprus reginae*	Low
Reptile	*Imantodes cenchoa*	Low
Reptile	*Leptodeira annulata*	Low
Reptile	*Liophis miliaris*	Low
Reptile	*Liophis poecilogyrus*	Low
Reptile	*Lygophis meridionalis*	Very high
Reptile	*Oxyrhopus guibei*	Very high
Reptile	*Oxyrhopus trigeminus*	Medium
Reptile	*Philodryas aestiva*	Very high
Reptile	*Philodryas agassizii*	Very high
Reptile	*Philodryas nattereri*	Low
Reptile	*Philodryas olfersii*	Very high
Reptile	*Philodryas patagoniensis*	Very high
Reptile	*Pseudoboa nigra*	Very high
Reptile	*Rhachidelus brazili*	High
Reptile	*Sibynomorphus mikanii*	Low
Reptile	*Simophis rhinostoma*	High
Reptile	*Tantilla melanocephala*	Very high
Reptile	*Dryophylax hypoconia*	High
Reptile	*Thamnodynastes rutilus*	High
Reptile	*Xenodon merremii*	Medium
Reptile	*Micrurus frontalis*	Medium
Reptile	*Micrurus lemniscatus*	High
Reptile	*Bothrops alternatus*	Very high
Reptile	*Bothrops itapetiningae*	Very high
Reptile	*Bothrops moojeni*	Very high
Reptile	*Bothrops neuwiedi*	Very high
Reptile	*Crotalus durissus*	Very high
Reptile	*Ophiodes fragilis*	Very high
Reptile	*Ophiodes striatus*	Very high
Reptile	*Hemidactylus mabouia*	High
Reptile	*Cercosaura ocellata*	High
Reptile	*Cercosaura schreibersii*	Very high
Reptile	*Anisolepis grilli*	Low

Reptile	*Polychrus acutirostris*	Medium
Reptile	*Aspronema dorsivittatum*	Very high
Reptile	*Copeoglossum nigropunctatum*	Medium
Reptile	*Manciola guaporicola*	Very high
Reptile	*Notomabuya frenata*	Medium
Reptile	*Ameiva ameiva*	Very high
Reptile	*Cnemidophorus ocellifer*	Very high
Reptile	*Salvator merianae*	Very high
Reptile	*Stenocercus canastra*	Very high
Reptile	*Tropidurus itambere*	Very high
Reptile	*Acanthochelys spixii*	Indeterminate
Reptile	*Hydromedusa tectifera*	Indeterminate
Reptile	*Mesoclemmys vanderhaegei*	Indeterminate
Reptile	*Phrynops geoffroanus*	Indeterminate
Reptile	*Amphisbaena alba*	Low
Reptile	*Caiman latirostris*	Indeterminate
Reptile	*Paleosuchus palpebrosus*	Indeterminate
Amphibian	*Ischnocnema izecksohni*	Medium
Amphibian	*Ischnocnema juipoca*	Medium
Amphibian	*Rhinella diptycha*	Medium
Amphibian	*Rhinella rubescens*	Indeterminate
Amphibian	*Vitreorana eurygnatha*	Low
Amphibian	*Vitreorana franciscana*	Low
Amphibian	*Ameerega flavopicta*	High
Amphibian	*Boana albopunctata*	Low
Amphibian	*Boana cipoensis*	Low
Amphibian	*Boana faber*	Medium
Amphibian	*Boana lundii*	Low
Amphibian	*Bokermannohyla circumdata*	Low
Amphibian	*Bokermannohyla ibitiguara*	Low
Amphibian	*Bokermannohyla sazimai*	High
Amphibian	*Dendropsophus jimi*	Low
Amphibian	*Dendropsophus minutus*	Low
Amphibian	*Dendropsophus rubicundulus*	Low
Amphibian	*Ololygon canastrensis*	Low
Amphibian	*Ololygon machadoi*	Low
Amphibian	*Ololygon pombali*	Low
Amphibian	*Pithecopus ayeaye*	High
Amphibian	*Scinax fuscovarius*	High
Amphibian	*Scinax maracaya*	High
Amphibian	*Scinax pombali*	High
Amphibian	*Scinax squalirostris*	Low
Amphibian	*Crossodactylus franciscanus*	Low
Amphibian	*Crossodactylus trachystomus*	Low
Amphibian	*Odontophrynus carvalhoi*	Medium

Amphibian	*Odontophrynus monachus*	Indeterminate
Amphibian	*Proceratophrys cristiceps*	Medium
Amphibian	*Proceratophrys moratoi*	Indeterminate
Amphibian	*Ischnocnema juipoca*	Very high
Amphibian	*Leptodactylus cunicularius*	Very high
Amphibian	*Leptodactylus fuscus*	Very high
Amphibian	*Leptodactylus jolyi*	Very high
Amphibian	*Leptodactylus labyrinthicus*	Very high
Amphibian	*Leptodactylus latrans*	Indeterminate
Amphibian	*Leptodactylus mystacinus*	Medium
Amphibian	*Physalaemus cuvieri*	Very high
Amphibian	*Physalaemus nattereri*	Very high
Amphibian	*Pseudopaludicola saltica*	High
Amphibian	*Elachistocleis bicolor*	Very high
Amphibian	*Elachistocleis cesarii*	Very high
Amphibian	*Elachistocleis ovalis*	Very high
Amphibian	*Siphonops annulatus*	Indeterminate
Birds	*Crypturellus obsoletus*	Medium
Birds	*Crypturellus parvirostris*	Very high
Birds	*Crypturellus tataupa*	Medium
Birds	*Nothura maculosa*	Very high
Birds	*Nothura minor*	Very high
Birds	*Rhea americana*	Indeterminate
Birds	*Penelope obscura*	Low
Birds	*Penelope superciliaris*	Low
Birds	*Crax fasciolata*	Very high
Birds	*Cariama cristata*	Very high
Birds	*Vanellus chilensis*	Very high
Birds	*Columbina minuta*	High
Birds	*Columbina picui*	Very high
Birds	*Columbina squammata*	High
Birds	*Columbina talpacoti*	High

GENERAL CONCLUSIONS

The results of this dissertation highlight the impact of fire on vertebrates in Brazil, as well as the factors that modulate mortality, survival, and species resilience to this disturbance across different biomes and scenarios. Overall, small-bodied vertebrates (<1 kg) and reptiles were most negatively affected by fire, exhibiting high mortality, especially in the Pantanal. In contrast, larger species, such as mammals and birds (>7 kg), as well as reptiles that use underground refuges, showed higher probabilities of survival. These underground refuges, particularly abundant in grasslands, serve as key elements that support fauna persistence in areas subject to frequent fire regimes, such as Serra da Canastra National Park.

Furthermore, we found that fire-induced mortality compromises ecosystem services provided by mammals, including seed dispersal, disease control, and ecotourism, which in turn have implications for landscape structure and functionality, as well as for climate change adaptation and mitigation. Citizen science played a fundamental role in Chapters 1 and 2 by expanding the spatial coverage of these types of data and revealing sampling gaps that must be overcome to support improved management practices.

Based on the findings of this research, we recommend to:
(i) strengthen standardized data collection and sharing on fire-induced wildlife mortality and survival, encouraging citizen science and the creation of open-access repositories;
(ii) adopt mosaic prescribed burns that maintain landscape heterogeneity, avoiding vegetation homogenization and protecting refuges;
(iii) investigate the distribution and dynamics of refuge openings before and after fires, applying methods such as environmental DNA to identify species associated with each shelter;
(iv) integrate genetic and ecological approaches to understand population structure and species resilience to fire; and
(v) implement participatory public policies that balance biodiversity conservation with socioeconomic demands and traditional fire use.

In summary, this work reinforces that knowledge of fire impacts on animals is essential for conserving faunal biodiversity in a future increasingly shaped by more frequent and intense wildfires in both fire-dependent and fire-sensitive biomes. By integrating research, management, and social engagement, it will be possible to ensure the maintenance of biodiversity and ecosystem functionality across Brazilian ecosystems under global change.

BIBLIOGRAPHIC REFERENCES

BATISTA, Eugênia KL et al. In case of fire, escape or die: a trait-based approach for identifying animal species threatened by fire. **Fire**, v. 6, n. 6, p. 242, 2023. https://doi.org/10.3390/fire6060242

BANKS, Sam C. et al. Where do animals come from during post-fire population recovery? Implications for ecological and genetic patterns in post-fire landscapes. **Ecography**, v. 40, n. 11, p. 1325-1338, 2017. https://doi.org/10.1111/ecog.02251

BONTA, Mark et al. Intentional fire-spreading by "Firehawk" raptors in Northern Australia. **Journal of Ethnobiology**, v. 37, n. 4, p. 700-718, 2017. https://doi.org/10.2993/0278-0771-37.4.700

BOWMAN, David MJS et al. Fire in the Earth system. **Science**, v. 324, n. 5926, p. 481-484, 2009. https://doi.org/10.1126/science.1163886

BRANDO, Paulo Monteiro et al. Abrupt increases in Amazonian tree mortality due to drought–fire interactions. **Proceedings of the National Academy of Sciences**, v. 111, n. 17, p. 6347-6352, 2014. https://doi.org/10.1073/pnas.1305499111

COSTA, Bernardo Miglio et al. Direct and short-term effects of fire on lizard assemblages from a Neotropical savanna hotspot. **Journal of Herpetology**, v. 47, n. 3, p. 502-510, 2013. https://doi.org/10.1670/12-043

DÍAZ, Sandra et al. Pervasive human-driven decline of life on Earth points to the need for transformative change. **Science**, v. 366, n. 6471, p. eaax3100, 2019. https://doi.org/10.1126/science.aax3100

DOHERTY, Tim S. et al. Fire as a driver and mediator of predator–prey interactions. **Biological Reviews**, v. 97, n. 4, p. 1539-1558, 2022. https://doi.org/10.1111/brv.12853

DOS SANTOS, Ana Carla et al. Managing fires in a changing world: Fuel and weather determine fire behavior and safety in the neotropical savannas. **Journal of environmental management**, v. 289, p. 112508, 2021. https://doi.org/10.1016/j.jenvman.2021.112508

ENGSTROM, R. Todd. First-order fire effects on animals: review and recommendations. Fire **Ecology**, v. 6, p. 115-130, 2010. https://doi.org/10.4996/fireecology.0601115

GONZÁLEZ, Tania Marisol et al. Effects of fire history on animal communities: a systematic review. **Ecological Processes**, v. 11, n. 1, p. 1-11, 2022. https://doi.org/10.1186/s13717-021-00357-7

GRAFE, T. Ulmar; DOEBLER, Stefanie; LINSENMAIR, K. Eduard. Frogs flee from the sound of fire**. Proceedings of the Royal Society of London. Series B: Biological Sciences**, v. 269, n. 1495, p. 999-1003, 2002. https://doi.org/10.1098/rspb.2002.1974

HARDESTY, Jeff; MYERS, Ron; FULKS, Wendy. Fire, ecosystems, and people: a preliminary assessment of fire as a global conservation issue. In: **The George Wright Forum**. George Wright Society, 2005. p. 78-87. https://www.jstor.org/stable/43597968

HARMANGE, Clément et al. Fire shapes mammal abundance at the Cerrado-Pantanal ecotone: Scale of effect, species traits and land-cover interaction**. Journal for Nature Conservation**, v. 82, p. 126728, 2024. https://doi.org/10.1016/j.jnc.2024.126728

HE, Tianhua; LAMONT, Byron B.; PAUSAS, Juli G. Fire as a key driver of Earth's biodiversity. **Biological Reviews**, v. 94, n. 6, p. 1983-2010, 2019. https://doi.org/10.1111/brv.12544

JOLLY, Chris J. et al. Animal mortality during fire. **Global Change Biology**, v. 28, n. 6, p. 2053-2065, 2022. https://doi.org/10.1111/gcb.16044

JONES, Gavin M. et al. Fire-driven animal evolution in the Pyrocene. **Trends in Ecology & Evolution**, v. 38, n. 11, p. 1072-1084, 2023. https://doi.org/10.1016/j.tree.2023.06.003

KECK, François et al. The global human impact on biodiversity. **Nature**, p. 1-6, 2025. https://doi.org/10.1038/s41586-025-08752-2

KOBZIAR, Leda N. et al. Principles of fire ecology. **Fire Ecology**, v. 20, n. 1, p. 39, 2024. https://doi.org/10.1186/s42408-024-00272-0

LEWIS, Dyani. 'Deathly silent': Ecologist describes Australian wildfires' devastating aftermath. **Nature**, v. 577, n. 7790, p. 304-305, 2020. https://doi.org/10.1038/D41586-020-00043-2

MAGIOLI, Marcelo et al. Forest type modulates mammalian responses to megafires. **Scientific reports,** v. 14, n. 1, p. 13538, 2024. https://doi.org/10.1038/s41598-024-64460-3

MARENGO, Jose A. et al. Extreme drought in the Brazilian Pantanal in 2019–2020: Characterization, causes, and impacts. **Frontiers in Water**, v. 3, p. 639204, 2021. https://doi.org/10.3389/frwa.2021.639204

MENDYK, Robert W.; WEISSE, Adam; FULLERTON, Will. A wake-up call for sleepy lizards: the olfactory-driven response of Tiliqua rugosa (Reptilia: Squamata: Sauria) to smoke and its implications for fire avoidance behavior. **Journal of Ethology**, v. 38, n. 2, p. 161-166, 2020. https://doi.org/10.1007/s10164-019-00628-z

MICHEL, Alice et al. Integrating sensory ecology and predator-prey theory to understand animal responses to fire. **Ecology Letters**, v. 26, n. 7, p. 1050-1070, 2023. https://doi.org/10.1111/ele.14231

NEWSOME, Thomas M.; SPENCER, Emma E. Megafires attract avian scavenging but carcasses still persist. **Diversity and Distributions**, v. 28, n. 3, p. 515-528, 2022. https://doi.org/10.1111/ddi.13390

NIEMAN, Willem A. et al. A review of the responses of medium-to large-sized African mammals to fire. **African Journal of Range & Forage Science**, v. 39, n. 3, p. 249-263, 2022. https://doi.org/10.2989/10220119.2021.1918765

NIMMO, Dale G. et al. Animal movements in fire-prone landscapes. **Biological Reviews**, v. 94, n. 3, p. 981-998, 2019. https://doi.org/10.1111/brv.12486

NIMMO, Dale G. et al. Welcome to the Pyrocene: Animal survival in the age of megafire. **Global Change Biology**, v. 27, n. 22, p. 5684-5693, 2021. https://doi.org/10.1111/gcb.15834

NOWACK, Julia et al. Can hibernators sense and evade fires? Olfactory acuity and locomotor performance during deep torpor. **The Science of Nature**, v. 103, n. 9, p. 1-7, 2016. https://doi.org/10.1007/s00114-016-1396-6

PACHECO, Luis F. et al. Muerte de mamíferos por los incendios de 2019 en la Chiquitania. **Ecología en Bolivia: revista del Instituto de Ecología**, v. 56, n. 1, p. 4-16, 2021.

PALMER, Meredith S.; PACKER, Craig. Reactive anti-predator behavioral strategy shaped by predator characteristics. **PloS one**, v. 16, n. 8, p. e0256147, 2021. https://doi.org/10.1371/journal.pone.0256147

PAUSAS, Juli G.; KEELEY, Jon E. A burning story: the role of fire in the history of life. **BioScience**, v. 59, n. 7, p. 593-601, 2009. https://doi.org/10.1525/bio.2009.59.7.10

PAUSAS, Juli G.; KEELEY, Jon E. Wildfires and global change. **Frontiers in Ecology and the Environment**, v. 19, n. 7, p. 387-395, 2021. https://doi.org/10.1002/fee.2359

PAUSAS, Juli G.; PARR, Catherine L. Towards an understanding of the evolutionary role of fire in animals. **Evolutionary Ecology**, v. 32, n. 2, p. 113-125, 2018. https://doi.org/10.1007/s10682-018-9927-6

PIVELLO, Vânia R. et al. Understanding Brazil's catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. **Perspectives in Ecology and Conservation**, v. 19, n. 3, p. 233-255, 2021. https://doi.org/10.1016/j.pecon.2021.06.005

POCKNEE, Christopher A. et al. Modeling mammal response to fire based on species' traits. **Conservation Biology**, v. 37, n. 4, p. e14062, 2023. https://doi.org/10.1111/cobi.14062

PYNE, Stephen J. **The Pyrocene: How we created an age of fire, and what happens next**. Univ of California Press, 2022.

REGO, Francisco Castro et al. Fire effects on plants, soils, and animals. **Fire science: From chemistry to landscape management,** p. 259-318, 2021. https://doi.org/10.1007/978-3-030-69815-7_9

REGO, Francisco Castro et al. Fire regimes, landscape dynamics, and landscape management. **Fire Science: From Chemistry to Landscape Management**, p. 421-507, 2021. https://doi.org/10.1007/978-3-030-69815-7_12

SCOTT, Andrew C.; GLASSPOOL, Ian J. The diversification of Paleozoic fire systems and fluctuations in atmospheric oxygen concentration. **Proceedings of the National Academy of Sciences**, v. 103, n. 29, p. 10861-10865, 2006. https://doi.org/10.1073/pnas.0604090103

SEMEDO, T. B. F. et al. (2022). Escaping the flames. **Pantanal Science.** 7(1), 19-2. ISSN 2357-9056.

SOBREIRA, Ernandes et al. Wildfires and their toll on Brazil: Who's counting the cost?. **Perspectives in Ecology and Conservation**, 2025. https://doi.org/10.1016/j.pecon.2025.06.003

SOUZA, Clarice Vieira; LOURENÇO, Águeda; VIEIRA, Emerson Monteiro. Species-specific responses of medium and large mammals to fire regime attributes in a fire-prone neotropical savanna. **Fire**, v. 6, n. 3, p. 110, 2023. https://doi.org/10.3390/fire6030110

THAPA, Shyam Kumar et al. Fire and forage quality: Postfire regrowth quality and pyric herbivory in subtropical grasslands of Nepal. **Ecology and Evolution**, v. 12, n. 4, p. e8794, 2022. https://doi.org/10.1002/ece3.8794

TOMAS, Walfrido Moraes et al. Distance sampling surveys reveal 17 million vertebrates directly killed by the 2020's wildfires in the Pantanal, Brazil. **Scientific Reports**, v. 11, n. 1, p. 23547, 2021. https://doi.org/10.1038/s41598-021-02844-5

WHELAN, R. J. et al. Critical life cycles of plants and animals: developing a process-based understanding of population changes in fire-prone landscapes. In: R. A. Bradstock, J. E. Williams, & A. M. Gill (Eds.), **Flammable Australia: The fire regimes and biodiversity of a continent** (pp. 94–124). Cambridge University Press. 2002.

WU, Chao et al. Historical and future global burned area with changing climate and human demography. **One Earth**, v. 4, n. 4, p. 517-530, 2021. https://doi.org/10.1016/j.oneear.2021.03.002