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Risk and resilience: a review of functional traits influencing fire vulnerability in Pantanal mammals

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ABSTRACT – In 2020, the Brazilian Pantanal experienced unprecedented wildfires that burned approximately 40,000 km² and resulted in the death of an estimated 17 million vertebrates. This catastrophic event, characterized by an extreme fire behavior and large extension facilitated by a combination of accumulated organic matter and a prolonged drought, has highlighted both the acute vulnerability of the Pantanal's ecosystem to seasonal wildfires and the need for a comprehensive understanding of their potential effects on species and ecosystem dynamics. This study explores the vulnerability of mammals to wildfires in the Pantanal, focusing on the analysis of fire vulnerability traits and the spatial distribution of species. We reviewed a total of 2,868 studies published since 1938, focused on the physical attributes, behavioral patterns, and ecological dynamics of five mammalian orders: Artiodactyla, Carnivora, Didelphimorphia, Rodentia, and Perissodactyla. The analysis revealed a significant increase in research on fire vulnerability traits, particularly in carnivores, since the year 2000. The most studied traits include habitat preference, body size, and diet, while other critical

traits for understanding fire sensitivity received less attention, such as reproductive season, mobility, social behavior and body size. Our findings highlight a marked seasonality in fire regimes and habitat specialization among the Pantanal's mammal species, with a concerning overlap between the 2019-2020 wildfires and the distribution of several species, suggesting potential severe declines in the abundance and distribution. These findings advocate for immediate conservation efforts targeting key habitats and refined wildfire management approaches to mitigate impacts, particularly on geographically restricted species. It also calls for a more balanced research focus across different taxa and traits to fully understand the ecological roles and vulnerabilities of less-studied species in the face of increasing fire frequencies and intensities in the Pantanal biome.

Risco e resiliência: uma revisão dos atributos funcionais que influenciam a vulnerabilidade ao fogo em mamíferos do Pantanal

RESUMO – Em 2020, incêndios em vegetação queimaram aproximadamente 40 mil hectares e mataram 17 milhões de vertebrados. Esse evento catastrófico, caracterizado pelo comportamento extremo do fogo e facilitado pela combinação de matéria orgânica acumulada e seca prolongada, evidenciou tanto a vulnerabilidade do ecossistema pantaneiro frente aos incêndios sazonais quanto a necessidade de um entendimento mais amplo sobre seus possíveis efeitos na biodiversidade local e nas dinâmicas ecossistêmicas. Este estudo explora a vulnerabilidade dos mamíferos do Pantanal frente aos incêndios em vegetação, com foco nas características ecológicas e sua relação com o fogo e a distribuição espacial das espécies. Foram revisados 2.868 estudos publicados desde 1938, abarcando cinco ordens de mamíferos: Artiodactyla, Carnivora, Didelphimorphia, Rodentia e Perissodactyla. As análises revelaram um aumento significativo em pesquisas sobre a vulnerabilidade ao fogo, particularmente em carnívoros, a partir do ano 2000. As características mais estudadas incluem a preferência de *habitat*, tamanho corpóreo e dieta, enquanto outros aspectos críticos para entender a sensibilidade ao fogo receberam menos atenção, como época reprodutiva, mobilidade, comportamento social e tamanho corpóreo. Nossos resultados ressaltaram uma sazonalidade marcada de ocorrência do fogo em 2019-2020 e especialização de *habitat* entre as espécies de mamíferos do Pantanal, com uma sobreposição preocupante entre os incêndios desses anos e a distribuição de várias espécies, que pode influenciar em declínio significativo da abundância e distribuição. Os resultados apontam a necessidade esforços de conservação imediatos, com alvo em *habitat*-chave e abordagens de manejo do fogo direcionadas a mitigar os impactos na fauna, particularmente em espécies geograficamente restritas. Também indicam a necessidade de um maior equilíbrio no foco de pesquisas entre diferentes táxons e características a fim de entender plenamente as funções ecológicas e vulnerabilidades de espécies menos estudadas frente ao aumento da frequência e intensidade dos incêndios no bioma Pantanal.

Riesgo y resiliencia: una revisión de los rasgos funcionales que influyen en la vulnerabilidad al fuego en mamíferos del Pantanal

RESUMEN – En 2020, el Pantanal brasileño experimentó incendios forestales sin precedentes que quemaron aproximadamente 40.000 km² y provocaron la muerte de por lo menos 17 millones de vertebrados. Este evento catastrófico, caracterizado por un comportamiento extremo del fuego facilitado por una combinación de materia orgánica acumulada en áreas inundadas de larga duración, comunidades de macrófitos, alfombras flotantes, pastizales abiertos

y una sequía prolongada, ha destacado tanto la severa vulnerabilidad del ecosistema del Pantanal a los incendios forestales sazonales, como la necesidad de una comprensión integral de sus efectos potenciales sobre las especies y la dinámica del ecosistema. Este estudio explora la vulnerabilidad de los mamíferos a los incendios forestales en el Pantanal, centrándose en el análisis de los rasgos de vulnerabilidad al fuego y la distribución espacial de las especies. Revisamos un total de 2.868 estudios publicados desde 1938, que abarcan cinco órdenes de mamíferos: Artiodactyla, Carnivora, Didelphimorphia, Rodentia y Perissodactyla. El análisis reveló un aumento significativo en la investigación sobre los rasgos de vulnerabilidad al fuego, particularmente en carnívoros, desde el año 2000. Los rasgos más estudiados incluyen la preferencia de hábitat, el tamaño corporal y la dieta, mientras que otros rasgos críticos para comprender la sensibilidad al fuego recibieron menos atención. Nuestros descubrimientos destacan una sazonalidad acentuada en los regímenes de incendios y la especialización del hábitat entre las especies de mamíferos del Pantanal, con una superposición preocupante entre los incendios forestales de 2019-2020 y la distribución de varias especies, lo que sugiere posibles disminuciones severas en la abundancia y distribución. Los descubrimientos abogan por esfuerzos de conservación inmediatos dirigidos a hábitats clave y enfoques refinados de manejo de incendios forestales para mitigar los impactos, particularmente en especies geográficamente restringidas. También requiere un enfoque de investigación más equilibrado en diferentes taxones y rasgos para comprender completamente los roles menos estudiados frente al aumento de la frecuencia e intensidad de los incendios en el bioma del Pantanal.

Introduction

The Brazilian Pantanal, the largest flooded area in the word, faced an extreme wildfire event in 2020, where 40,000 km² were burned [1] and caused the death of an estimate 17 million vertebrates [2] Typically, seasonal wet-dry ecosystems like the Pantanal are prone to burning during the dry season because of the increased vegetative load sustained by flood-induced fertility [3][4]. But in 2020, the Pantanal had a large amount of accumulated organic matter in long-lasting flooded areas covered by macrophytes communities, floating mats and open grasslands subjected to vegetation encroachment and prolonged drought, which created a propitious scenario for a fire of extreme behavior [1][5]. The devastating intensity of these wildfires has emphasized the critical need for a more comprehensive understanding of the potential effects on species and ecosystem dynamics.

Fire has been widely accepted as an evolutionary force structuring biodiversity in fire-prone ecosystems [6]. While the interaction of fire with plants has been thoroughly explored in the scientific literature, knowledge about its effects on animals is still lacking [7][8]. The fire-related impacts on biodiversity will generally depend on several factors, including the spatial and temporal patterns of fire regime, as well as the type of vegetation and the inherent biological traits

of local species [9][10]. For the fauna, these impacts can be of three types [11]: 1) direct or first-order, those that occur during the fire or shortly after [11]; 2) indirect or second-order, which are related to the processes post-fire, such as resource availability, that will determine the viability of a surviving population [11]; 3) evolutionary, such as adaptations of a species throughout time to enhance its ability to persist in a habitat affected by recurrent fires [11].

Generally, the impact of a natural fire in an area adapted to and reliant on fire for its biodiversity and ecological processes tends to be minimal. Such fires typically result in low mortality and injuries among wildlife, while simultaneously providing benefits to numerous opportunistic animal species [12]. During a fire, predators often gain an advantage due to the increased availability of prey attempting to flee the flames [8]. After the fire, changes in the habitat structure can lead to harsher microclimatic conditions (such as higher temperatures and lower humidity), diminished food supplies (characterized by scarcity, reduced nutritional value, and less palatability), and altered interactions with other species, including increased competition, predation risks, and parasitism [11]. Also, the simplified landscape increases the visibility of prey and the abundant supply of animal carcasses killed by the fire provides sustenance for scavengers [13]. Plants resprouting attract herbivorous species,

while mass flowering events attract the attention of pollinators and their respective predators. In the long-term, while no species is entirely immune to fire effects, certain behavioral and physical adaptations can enhance some animals' survival chances, particularly against fires of lower intensity. Although most of existing research focuses on plants [8][14], there is already evidence of some morphological adaptations in animals such as the development of cryptic coloration that provides camouflage in the new environment [15].

Nevertheless, changes in global fire regimes due to human activities are leading to a rise in extreme events, even in ecosystems that are used to and depend on fire. This shift can compromise the predictability of these ecosystems, affecting their stability and the species that rely on them [16][17]. In such scenarios, the situation changes dramatically, leading to significantly high rates of mortality, injuries, and cases of intoxication (direct effects), often alongside a scarcity of food and/or water, and the absence of shelter or refuges in the aftermath of the fire (indirect effects). Consequently, the populations that do survive may struggle to recover adequately. Moreover, given the rapid pace of these changes, it's plausible that many animal species will not have sufficient time to adapt in order to ensure their survival (evolutionary effects). In this article, we aim to describe the mammal community of Pantanal in terms of their physical, biological, and behavioral traits, assuming that these factors can either amplify or reduce their sensitivity to fire and chances of survival.

Material and Methods

We employed the Web of Science database (www.isiknowledge.com) to access publications that address functional traits related to fire sensitivity for the 76 mammal species that inhabit the Pantanal and were listed for this study (Figure 1). Our search included all books, book sections, conference papers, and journal articles from 1938 to 2023, focusing on titles, keywords, and abstracts. We eliminated duplicates, and publications in disciplines like genetics, paleontology, biochemistry, anthropology, microbiology, epidemiology, parasitology, and medicine were omitted because they do not align with the objectives of this study.

In addition to the Web of Science, we also utilized the Salve platform to gather information (https://Salve.icmbio.gov.br). The Salve platform is a comprehensive database managed by the Chico Mendes Institute of Biodiversity Conservation (ICMBio), which provides detailed data on Brazilian biodiversity, including species distribution, conservation status, and ecological information. This resource was particularly valuable for obtaining localized and species-specific data relevant to the 76 mammal species listed for this study.

We used keywords to conduct the search and systematically categorized the ecological and biological traits of species associated with their sensitivity or resilience to fire (Supplementary Material). Our categorization included aspects such as endemism, distinguishing between species restricted to Brazil's Pantanal and those with wider distributions. We also examined habitat types, identified using Salve data, to assess habitat specialization. This included natural forests, savannas, grasslands, wetlands, planted forests, pastures, agricultural areas, agricultural-pasture mosaics, and urban infrastructure. Body mass and body size were classified into small (<1kg), medium (1-7 kg), and large (>7 kg) categories, while population dynamics were represented by the intrinsic growth rate, indicating species' replacement capacity. We differentiated ecological functions or feeding habits among various types such as browsers, large seed dispersers, predators of medium and large vertebrates, seed predators, grazers, dispersers of small seeds, predators of small vertebrates, predators of invertebrates, and scavengers. Mobility was considered to infer survival chances and escape strategies, classifying species as arboreal, flying, semi-fossorial, fossorial, scansorial, terrestrial, semi-aquatic, or aquatic. Breeding season was categorized as undefined, rainy season, early dry season, or late dry season. Reproductive stage and nesting behavior included aspects like courtship, mating, nesting, pregnancy, parental care, and breastfeeding. Reproductive biology was analyzed through sexual maturity, generational time, gestational period, and offspring average size. Home range was measured in square kilometers, and territorial behavior was distinguished between territorial and non-territorial. Movement behavior was classified as migratory, nomadic, or resident. Activity pattern was defined as nocturnal, crepuscular, diurnal, or cathemeral. Demography assessed species abundance as abundant, moderate, or rare. Escape strategy considered the most probable escape decision, such as running, climbing, swimming, taking refuge in dense forests, crevices, burrowing, or seeking refuge in vegetation. Social organization was defined as

A World Heritage Site and Biosphere Reserve under threat

In 2020, unprecedented wildfires in the Brazilian Pantanal burned around 40,000 km² and killed an estimated 17 million vertebrates, highlighting the ecosystem's extreme vulnerability to seasonal fires due to a combination of accumulated organic matter and prolonged drought.

CUIABÁ

BRAZIL

BOLIVIA

PARAGUAY

CAMPO GRANDE

PROTECTED AREAS

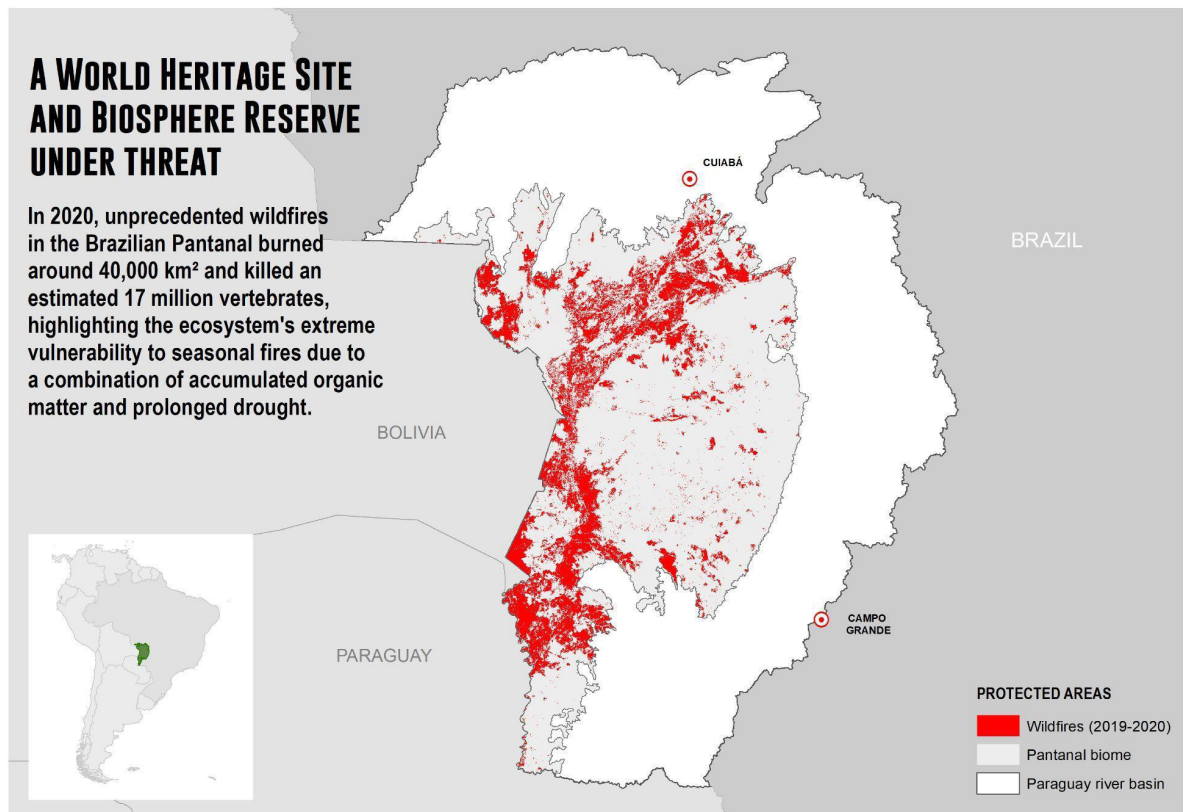Wildfires (2019-2020)
Pantanal biome
Paraguay river basin

Figure 1 – Pantanal biome's location in Brazil and South America, and the areas affected by fire in 2019 and 2020.

solitary or gregarious. This comprehensive approach provided a nuanced understanding of species' traits and their relative fire sensitivity.

Geographical distribution data for the 76 species were obtained from the Salve platform. These polygons were applied to the MapBiomas Project Collection 6's land cover and land use maps as a mask, delineating the habitats for each species. Additionally, the polygons were used to estimate the fire impact within each habitat category for the years 2019 and 2020. We downloaded the fire data from the MapBiomas Fogo Collection 1. The aforementioned MapBiomas datasets are accessible on the Google Earth Engine platform (https://brasil. mapbiomas.org/colecoes-mapbiomas/). For each species, we calculated the average area impacted by wildfires over the two years, categorizing the results by habitat type. This average was then converted into a percentage for a clear, comparative representation of the data.

Results and Discussion

Literature review

After excluding duplicates, we identified 2,868 studies published since 1938, distributed across the five orders as follows: Artiodactyla – represented by the families Cervidae and Tayassuidae (348 studies), Carnivora – represented by the families Felidae, Canidae, Mustelidae, and Procyonidae (1,703 studies), Didelphimorphia – represented by the family Didelphidae (342 studies), Rodentia – represented by the families Caviidae, Cricetidae, Ctenomyidae, Cuniculidae, Dasyproctidae, Echimyidae, Erethizontidae and Sciuridae (389 studies), and Perissodactyla – represented exclusively by the Tapiridae family (86 studies). All studies used in this work are listed in the supplementary material.

Within the Artiodactyla, two species garner significant attention in the literature: *Dicotyles tajacu*

and *Tayassu pecari*. Among carnivores, felids and canids are generally more thoroughly researched, with *Puma concolor* and *Panthera onca* standing out. In the Didelphimorphia order, *Monodelphis domestica*, *Didelphis albiventris*, and *Didelphis marsupialis* are among the most studied. The Perissodactyla order has a sole representative: *Tapirus terrestris*, which is generally well-researched. Meanwhile, within Rodentia, notable species include *Cuniculus paca*, *Hydrochoerus hydrochaeris*, *Cavia aperea*, *Akodon montesis*, and *Necromys lasiurus*.

The volume of research exploring fire-vulnerability traits has increased significantly since 2000, with particular emphasis on carnivores (Fig. 2a,b). This trend is unsurprising given the heightened concerns about its conservation status and a corresponding scientific desire to understand its ecological role. However, this raises questions regarding the comparatively limited attention given to other taxonomic orders, which could potentially hinder our ability to fully grasp how these less-studied species cope with wildfires.
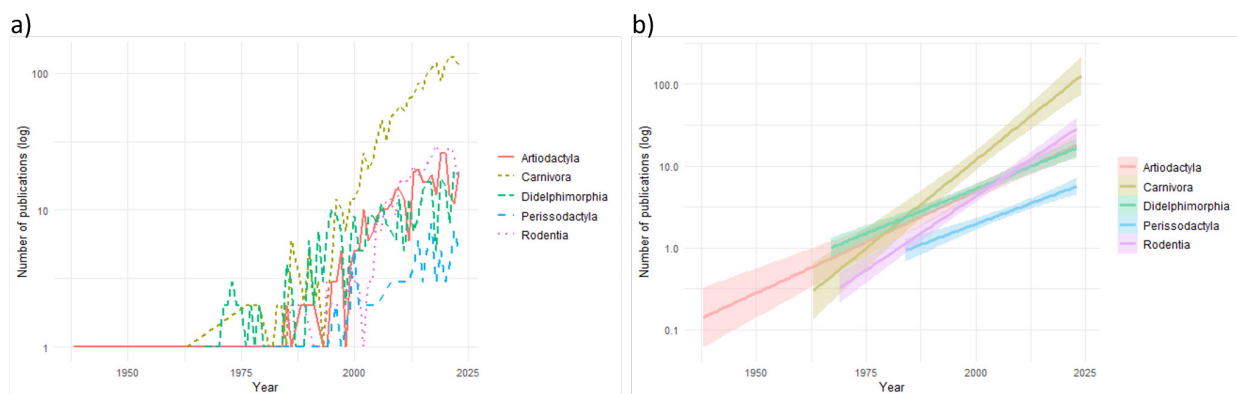

Figure 2 – Number of publications and trends up to 2023 categorized by order (a and b respectively).

Likewise, some traits have received more attention than others in scientific literature. Habitat preference, for example, emerges as the most frequently mentioned trait (2575 studies), followed by body size (2289), diet (2004), territorial behavior (1091), locomotion (509), home range (502), activity pattern (263), reproductive stage (248), population dynamics (226), social organization (172), movement behavior (150), reproductive biology (127), territorial behavior (56), and breeding season (52). This draws attention to information gaps that could be valuable in helping us identify species most sensitive to fire and develop effective management strategies aimed at their conservation.

Species and traits

After conducting a more detailed analysis of the publications, we observed a trend towards habitat

specialization among the mammals of the Pantanal. Around 37% of the species are found exclusively in forest ecosystems and another 5% in wetlands (Figure 3). These findings highlight the urgent need for conservation efforts focused on key habitats (forests and wetlands) that provide essential resources and structure for most of the biome's mammalian species, including habitat specialists [18].

A particularly concerning issue is the high level of overlap between the 2019-2020 wildfires and distribution of many species, potentially translating into major declines in abundance and distribution. For example, of the 76 species, 44 had 5-10% of their habitat burned, 12 had 10-15% of habitat burned and 8 had 15-20% of habitat burned (Figure 3). Within the group, there are two endemic species from the Rodentia order and ten species from both the Rodentia and Didelphimorphia orders that are geographically restricted. *Holochilus chacarius* and

Oligoryzomys chacoensis, both restricted to the Pantanal, had 16% and 11% of their habitats burned, respectively.

Ten other species are included in one of the threat categories of the Brazilian System of Biodiversity's Extinction Risk Assessment (Salve) (Brasil, 2022; Salve, 2024). For instance, *Puma concolor*, classified as Near Threatened (NT), experienced habitat burns of 14%. In the Vulnerable category (VU), *Chrysocyon brachyurus* had 9% of its habitat affected, *Lycalopex vetulus* 15%, *Herpailurus yagouaroundi* 13%, *Leopardus wiedii* 7%, *Panthera onca* 15%, *Speothos venaticus* 6%, *Tapirus terrestris* 9%, *Tayassu pecari* 6% and *Pteronura brasiliensis* 5%. However, one species categorized as Endangered (EN), *Leopardus braccatus* (ICMBio, 2024 – unpublished data), raises increased concern due to its threat level, with 16% of its habitats impacted by the 2020 wildfires. Additionally, it's crucial to emphasize that *Leopardus wiedii*, *Tayassu pecari*, and *Pteronura brasiliensis* are specialists in forests or wetlands, which means that any impact of fire on their living areas can be exacerbated by the species' inability to find suitable conditions and resources in other environments.

Another concerning issue is the consistently larger proportion of the range affected by fires in the late-dry season compared to the wet and early dry seasons for all the species (Figure 4). Although this data is not surprising, it emphasizes the critical need of a more consistent fire management in the Pantanal biome. Fires occurring late in the dry season tend to be more intense and severe [19]. As a result, the most sensitive wildlife may experience significant population declines. For instance, small and medium-sized species that seek refuge in clumps of vegetation, small trees or attempt to flee the fire by running, such as *Calomys callosus*, *Cavia aperea*, *Leopardus braccatus*, *Metachirus myosuros*, *Metachirus nudicaudatus, Monodelphis domestica, Oecomys franciscorum, Philander canus, Procyon cancrivorus, Thrichomys fosteri,* and *Thylamys macrurus*, might not be able to escape from severe fires [20].

In terms of spatial distribution, studies have revealed that the vast majority of mammal species within the Pantanal (across the Orders examined) have a widespread distribution, encompassing 83% of the total species richness. Meanwhile, about 17%

of these species are confined to the Pantanal within Brazil's borders, making them particularly vulnerable to large-scale wildfires.

Regarding body size, most species are classified as small-bodied (less than 1 kg), constituting 60% of the total. Meanwhile, medium (between 1-7 kg) and large-bodied (over 7 kg) species each comprise 20% of the population. Being small may offer some evolutionary advantages for surviving fires, given that small animals are more adept at finding small refuges, such as tiny burrows in the ground, small cracks in rocks, or small holes in tree trunks [21]. However, their reduced mobility may increase the risk of mortality during escape attempts or if a safe refuge is too distant to access promptly [22]. Furthermore, small-sized animals could be at a higher risk of predation in the more open landscape that emerges after a fire [13].

About 51% of mammal species are terrestrial, while 19% are arboreal, and 14% are scansorial. Arboreal and scansorial animals are capable of climbing trees or moving on the ground, enhancing survival chances when the fire exhibits less extreme behaviors. High-intensity fires can even kill individuals at the tops of the tallest trees through heat radiation or intoxication from toxic smoke [23]. Only 10% of the species are classified as semi-aquatic, fossorial (burrowing), or semi-fossorial. These adaptations may offer significant benefits for an individual during a wildfire. For example, semi-aquatic species might find refuge in water bodies, whereas fossorial and semi-fossorial species can escape the heat and flames by retreating into burrows or underground shelters they or others have created, potentially reducing their exposure to direct fire and its immediate effects [24][25].

In the context of dietary habits, 35% of species are small seed dispersers, making this the most common ecological function, followed by those that prey on invertebrates (21%). Species preying on small vertebrates comprise 14% of the population, with herbivorous browsers at 13%, and grazers at 3%. Species classified as predators of medium to large vertebrates, along with large seed dispersers and seed predators, each represent smaller segments of the ecosystem, at 3%, 2%, and 2% respectively. Notably, a significant portion of these species adopts a varied diet, encompassing more than one type of dietary habit.
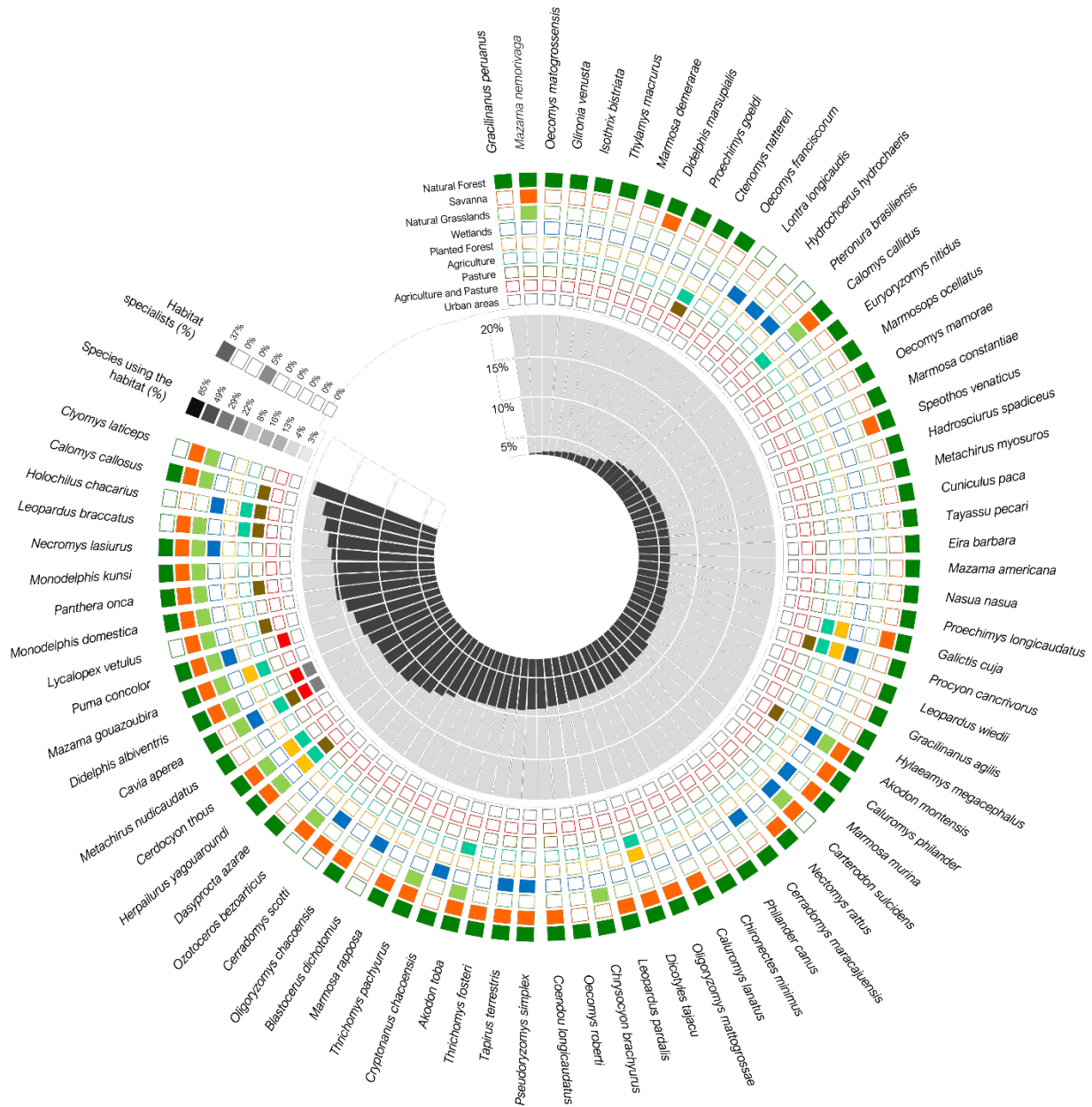
Figure 3 – The colored squares around the circle indicate the preferred habitats for each mammal species, with each color representing a specific type of habitat, such as forests, savannas, wetlands, and others. The two grayscale columns located further inside represent: (1) the percentage of species that use each habitat type (inner column) and (2) the percentage of species that are exclusive or specialists in these habitats (outer column). The black bars in the inner circle show the percentage of preferred habitat that was burned during the 2019-2020 fires.

Even though there are no species strictly categorized as obligate scavengers, some species such as *Panthera onca*, *Puma concolor*, *Lycalopex vetulus*, *Chrysocyon brachyurus*, *Cerdocyon thous*, *Didelphis albiventris,* and *Leopardus pardalis* can opportunistically feed on carcasses [26][27][28]. Small seed dispersers (or predators), invertebrate predators, grazers, and browsers may find an enhanced availability of food resources in the aftermath of a fire [29]. This includes the proliferation of herbaceous plants that produce

flowers, fruits, and seeds; open areas with few shrubs providing an ideal foraging ground for low xeric insectivores; improved visibility of small prey; and an abundance of regrowth for grazers and browsers to feed on [30][31][32]. In the simplified landscape following a fire, prey can spot predators from long distances, enhancing their chances of responding and escaping. Therefore, predators of large and medium-sized vertebrates may need to wait until prey availability and vegetation structure create the optimal environment for hunting [30].

Our research indicates that most species are diet-generalists. Approximately 76% have assorted eating habits, which could afford them some advantage in environments where their primary food sources are scarce [33]. About 3% of the species have an unknown dietary habits, and 21% are diet-specialists, which suggests they might be temporarily absent from the affected area until their resources are reestablished or die due to starvation. However, of the 16 diet-specialist species, 11 are small seed dispersers, two consume leaves, shoots, stems, barks, roots, and flowers of trees and shrubs, and three specialize in invertebrate predation. These food resources are expected to reappear in the landscape soon after a fire, highlighting the mammalian fauna's adaptability and resilience in their dietary habits.

While data on the threat level posed by fire seasonality is lacking for many species (28%), a significant portion appears to be at risk due to factors such as the timing of offspring birth or reproductive season coinciding with the late dry-season (August-October). During this period, fires are typically more intense and severe, making it challenging for the most vulnerable individuals, like juveniles, pregnant, or lactating females, to flee and survive [34]. *Cavia aperea, Cerradomys scotti, Chrysocyon brachyurus, Procyon cancrivorus,* and *Tayassu pecari* are species whose reproductive period is closely synchronized with the dry season, making them especially vulnerable to late-season fires.

Despite a significant information gap regarding territorial and movement behaviors, with 58% of species lacking data, those exhibiting strong site fidelity may perceive the risk of leaving their territory or home range to find unburned areas as more dangerous than remaining in a familiar site, even if it means facing limited or non-existent food sources [35]. As a result, these species could suffer from negative demographic impacts if their usual habitats are destroyed by fire. Around 33% of mammal species in the Pantanal are known to engage in territorial behavior, while only 8% tend to be non-territorial.

Among the orders examined, there are no migratory mammal species, but approximately 18% of the species are nomadic. Resident species make up about 14%. Nomadic species, which move irregularly across large areas in search of food, water, or breeding sites, may be better equipped to avoid localized threats such as fires by relocating to safer territories [36][37]. In contrast, resident species, which tend to stay within a defined home range, may face greater challenges during environmental disturbances, relying heavily on the resilience of their established habitats for survival.

Most species exhibit a crepuscular (12%) or nocturnal (45%) circadian rhythm. This trait could offer benefits, allowing individuals to be active when fires are milder and seek shelter during periods of heightened fire intensity. However, if their hiding spots, such as leaf litter, bushes, grasses, shallow burrows, or logs on the ground, are prone to burn, these species could be at risk of perishing in daytime fires [38][39]. Conversely, cathemeral (4%) and diurnal species (18%) might have the advantage of noticing an oncoming fire in time to flee, increasing their survival prospects. Despite its potential importance, the study of circadian cycles in these species is lacking, with 21% of species data deficient, suggesting that understanding these patterns could play a crucial role in informing fire management strategies.
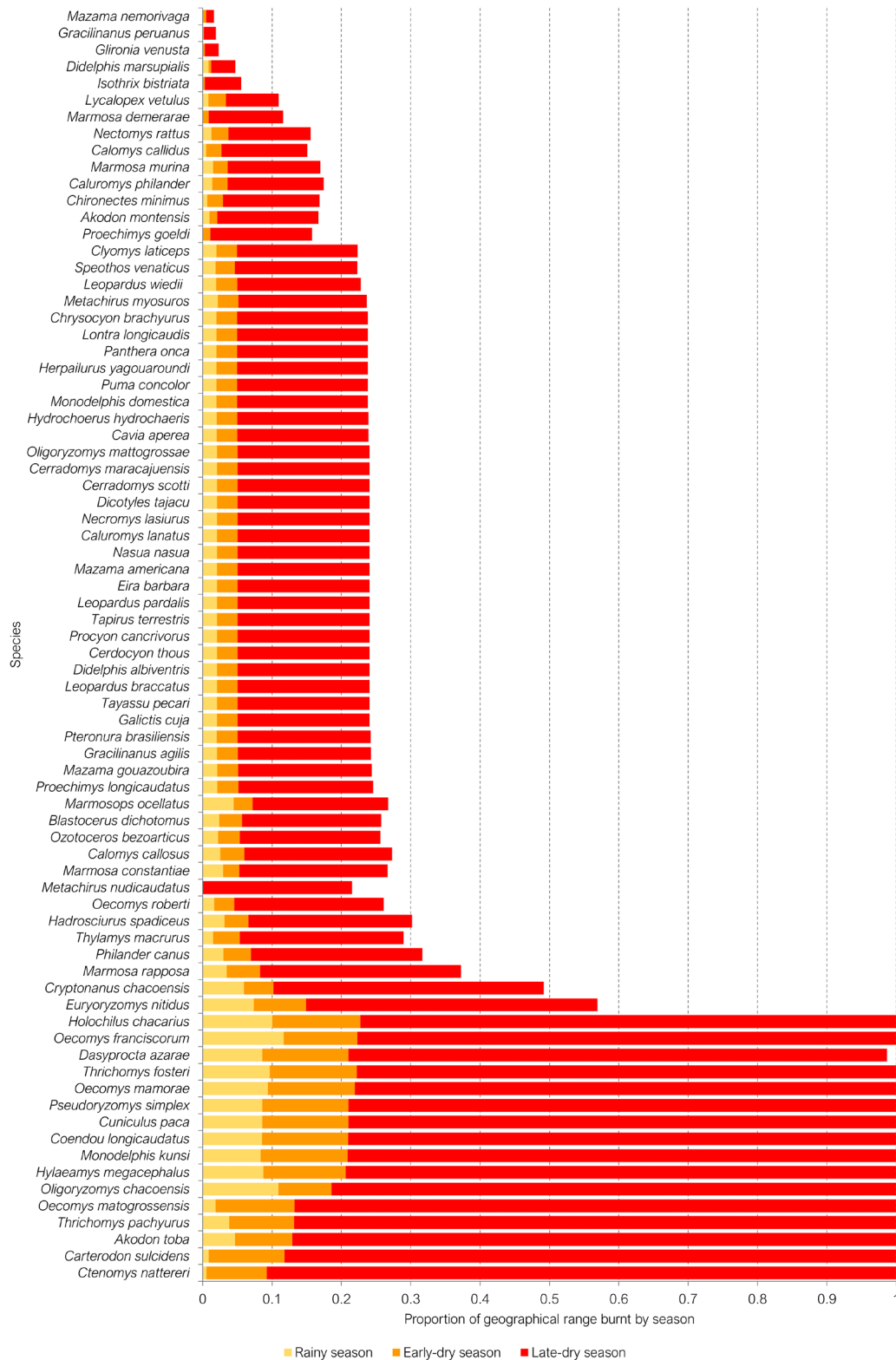
Figure 4 – Proportion of geographical range burned by season for each species. Light yellow bars represent fires in the rainy season. Orange bars represent early dry season fires and red bars represent late dry season fires.

When faced with wildfires, species' survival strategies can vary greatly, with their choices potentially enhancing or diminishing their likelihood of survival. Fire escape behaviors are poorly known and in general are not directly studied. However, they can be inferred from predator escape behavior,

types of habitat, locomotion, and other traits. For that reason, our findings may not be entirely accurate as they are based on assumptions. It is presumed that some species may attempt to escape wildfires by running or jumping over flames (28%). Among these species, four are small in size – *Cavia aperea*, *Metachirus* sp.*, Philander canus*, and *Thylamys macrurus*. Given their smaller size, these species have more limited mobility, which could potentially impact their ability to escape from fast-spreading fires. This limitation underscores the particular vulnerability of small runners to wildfires, as their options for evading danger are constrained by their physical capabilities. Around 8% of the species are likely to seek refuge in water, as they are typically aquatic or semi-aquatic, dwelling in burrows along the banks of watercourses and often using water as a means of escape from predators. These species, adapted to life in and around water, may have a survival advantage in such events by leveraging their natural habitat as a protective barrier against the flames. Approximately 17% of species are likely to employ tree climbing as a survival strategy during wildfires, while another 6% might opt for hiding within dense vegetation, and 13% may burrow into the ground or find safety in holes within living tree trunks. In contrast, a smaller fraction, about 3% of species, are expected to seek refuge in areas that are inherently safer from fires, such as forests, rocky areas, or crevices. The success of wildlife escape methods greatly varies with fire intensity and behavior. For instance, tree-dwelling or climbing species may evade surface-level fires, but intense blazes can significantly increase their risk of death, either from direct heat exposure or smoke inhalation. Larger animals have the ability to flee or even leap over fires, yet rapid fire spread can trap them, impairing their ability to navigate due to reduced visibility and disorientation [24]. Smaller creatures often seek refuge in underground burrows, a tactic that is effective in many fire-adapted environments [21][44]. However, in the face of intense fires, these small animals are also vulnerable to dangers such as smoke inhalation or increased predation in the altered, post-fire environment.

Approximately 40% of species in the study are solitary, while 9% show gregarious (group-living) behavior. Being part of a social group can significantly enhance survival chances during fires [40]. In a group, individuals can afford to lower their guard somewhat, without greatly increasing their personal risk, thanks to the safety net provided by collective vigilance [40]. As group size increases, individual vigilance may decrease, but the group's overall ability to detect threats improves due to the "many eyes" effect, which helps in scanning for danger more efficiently [40]. Effective collective threat detection relies on at least one group member remaining vigilant to identify potential dangers, such as an approaching fire, and then alerting the rest through various means like seeking shelter, fleeing, or making alarm calls. Fear and alertness can spread contagiously within a group, enabling even those who haven't directly spotted the danger to react and escape based on the group's collective awareness [41][42][43]. Hence, the dynamics of social organization, including group size, relational structure, and communication mechanisms, are crucial in enhancing the effectiveness of collective responses to fire threats.

Conclusion

This study offers a broad review of research on mammalian species in Brazil, specifically targeting the Pantanal biome and examining how these species probably interact with wildfires. We have found 2,868 studies identified since 1938, covering five major orders of mammals. The majority of these studies have focused on carnivores, indicating a strong scientific interest in understanding the ecological function and conservation needs of this group, likely driven by concerns over their conservation status. It is imperative to extend research efforts towards those species and traits that have been less studied.

The clear tendency towards habitat specialization among Pantanal mammal species highlights the need to protect forests and wetlands from fire. Not only for the survival of habitat specialists but also because these environments provide predictable and permanent shelter during fire events. The wildfires of 2019-2020 scorched a substantial portion of natural habitats, heightening concerns for species with limited geographical distributions and those listed as endangered or vulnerable in the Brazilian List of Endangered Species. This situation underscores the urgent need for targeted conservation efforts and enhanced protective measures for these at-risk species, especially considering the potential for future events of similar or greater magnitude. Understanding the specific vulnerabilities of these species to fire and habitat loss is crucial for developing effective strategies to mitigate impacts and ensure their long-term survival in their natural environments.

In conclusion, we strongly recommend the urgent implementation of a nuanced approach to fire management in the Pantanal within the framework

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of integrated fire management, articulated with environmental conservation and socio-economic sustainability [3][45]. A landscape-level strategy is imperative, taking into account the Upper Paraguay River Basin, as the headwaters of the main watercourses lie outside the established boundaries of the biome, significantly impacting flood levels. It is also essential to consider all interests and stakeholders in fire use, aiming to regulate it while protecting sensitive physiognomies, such as forests, in a fire-prone ecosystem with species adapted to natural fire regimes.

Ethical standards

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