

Article

Species-Specific Responses of Medium and Large Mammals to Fire Regime Attributes in a Fire-Prone Neotropical Savanna

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Abstract: Fire occurrence affects the distribution of key resources for fauna in natural ecosystems worldwide. For fire management strategies adequate for biodiversity conservation, the understanding of how species respond to fire-induced changes is essential. In this study, we investigated the role of fire regimes on spaces used by medium and large mammals at multiple spatial scales (0.8 ha to 78.5 ha) in a fire-prone savanna ecosystem (Brazilian Cerrado). We sampled mammals using 60 camera traps distributed in 30 sampling units located in grassland and typical savanna formations. We applied single-species occupancy models and AIC-based model selection to assess how mammals use the space in response to pyrodiversity (both diversity of fire frequencies and diversity of fire ages), the proportion of recently burned area, and the proportion of long-unburned area while accounting for detectability. Our results showed that fire regime variables affected the study species differently. Deer species used the space regardless of mosaic pyrodiversity and the proportion of specific fire ages. Fire-related variables, however, affected space use by tapirs and maned wolves. Tapirs preferred to use fire mosaics with lower diversity of fire frequencies, whereas maned wolves more intensively used mosaics with high fire age diversity and a high proportion of recently burned areas. Based on our findings, we recommend that fire management targeting specific mammal species should not necessarily focus on maximum pyrodiversity. Instead, we suggest a management strategy combining “patch mosaic burning” with the maintenance of specific fire-age patches suitable for different species’ requirements.



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Keywords: fire mosaic; habitat use; pyrodiversity; herbivores; carnivores; tropical savanna; fire management

1. Introduction

Habitat use by animals is affected by several factors, including the distribution of food resources, the occurrence of potential predators and competitors, and vegetation cover [1–7]. The distribution and effects of these factors, however, may be altered by disturbance events [8], affecting space use by the animals [9]. In fire-prone ecosystems, fire is a common disturbance that modifies vegetation structure and resource availability [10–14]. Understanding how species respond to these fire-induced changes is fundamental, considering the increase in large severe wildfires worldwide [15,16]. Such knowledge may contribute to the establishment of fire management strategies adequate for preventing large wildfires while creating fire mosaics more suitable for species conservation [17–19].

For fire management to be an efficient tool in protecting biodiversity, a management strategy must create relevant fire mosaics where species can thrive [20]. Many fire management programs are based on the establishment of heterogeneous fire mosaics to promote community biodiversity (“patch-mosaic burning”) [21–23]. This strategy follows the “pyrodiversity begets biodiversity” hypothesis, which proposes a relationship between spatial variation in successional stages post-fire and more diverse communities [24]. At the population level, some species also seem to be positively affected by pyrodiversity [25–27].

However, the empirical support for these positive effects on communities and populations is not consistent across ecosystems and taxa [27–30]. An alternative strategy is to keep large portions of areas with specific fire ages, i.e., the number of years since the last fire [20]. Some studies report a positive effect on species when long-unburned or recently burned areas are retained [31–33]. These studies indicated the extent of areas with specific fire ages as a better predictor for fire-induced faunal responses than pyrodiversity. Considering this variation in key fire-related factors affecting animals and context-specific faunal responses to distinct management strategies, the establishment of fire management actions must be based on the knowledge of local fire regime characteristics and how animal populations react to such characteristics.

In fire-prone ecosystems, terrestrial mammals are generally markedly affected by fire events [30,33–35]. For predators, fire-induced responses are driven mainly by changes in prey availability, hunting success, and habitat cover [36]. Furthermore, responses to habitat cover change can be regulated by species hunting strategies. While ambush predators may prefer long-unburned areas with more structured vegetation [37,38], cursorial species may select open habitats found in recently burned areas [38–40]. Burning may also affect large herbivores. This group may use recently burned areas more intensively in searching for high-quality forage [41,42] or avoid them when predators [43] or competitors [44] are attracted to these areas. The effects of areas with different fire ages within the landscape (i.e., pyrodiversity) on mammal space use seem to be variable. In Australia, for instance, the presence of a large carnivore (dingo) [25] and large marsupials [45] was higher in pyrodiverse areas. On the other hand, in North America, the abundance (an indicator of space use) of coyotes was lower in highly pyrodiverse areas [30]. Such negative effects of pyrodiversity may result from strong associations between species and specific fire regimes [46,47], whereas positive effects may arise when species use multiple patches of the fire mosaic landscape [48].

Mammals may respond to pyrodiversity or fire age from site-scales (up to 1 ha) [25,49] to landscape-scales [30,50]. This suggests that the fire mosaic pattern may affect mammal space use related to home range, habitat, and microhabitat selection (2nd, 3rd, and 4th habitat selection orders, respectively, sensu [51]). This variation highlights the necessity of evaluating fire effects in multiple spatial scales.

In this study, we investigated fire, and the use of habitat by medium and large terrestrial mammals in the Cerrado (neotropical savanna). We evaluated the potential effects of pyrodiversity and the proportion of recently burned and long-unburned areas on space use by these animals. Our objective was to identify the role of pyrodiversity (fire frequency diversity and fire age diversity), the proportion of recently burned areas, and the proportion of long-unburned areas in relation to the total available area on space use by mammals while accounting for detectability. If pyrodiversity is relevant for mammalian occurrence, we expect a positive effect of diversity of fire frequency and fire age on space use by large mammals. A pyrodiverse landscape would offer a greater variety of resources [52,53] and the opportunity for species to use these resources in a complementary way [54]. If the proportion of recently burned and long-unburned areas is important, we predict a positive effect of recently burned areas on the occurrence of mammals. These areas may offer better quality foraging for herbivores [42], adequate hunting habitats for cursorial predators [38], and facilitate the movement of cursorial species [54]. Considering that mammal responses to the predictor variables are potentially affected by the spatial scale considered [49], we tested these responses for three distinct spatial scales (from 0.8 ha to 78.5 ha).

2. Materials and Methods

2.1. Study Area and Species

We conducted fieldwork in the Chapada dos Veadeiros National Park (CVNP), a protected area of 240,000 ha located in the state of Goiás, Brazil (Figure 1). This region has a tropical climate, with the dry season occurring in winter according to the Köppen-Geiger classification [55]. The average annual temperature is 23.4 °C, with the highest average

temperature recorded in October (monthly average = 25.3 °C) and the lowest average temperatures observed in June and July (monthly average = 20.8 °C) [56]. The average annual rainfall is 1500 mm. Its distribution throughout the year defines two climatic seasons: the dry season, with mean monthly precipitation of 23.2 mm (between May and September), and the wet season, with mean monthly precipitation of 197.6 mm (between October and April) [56].

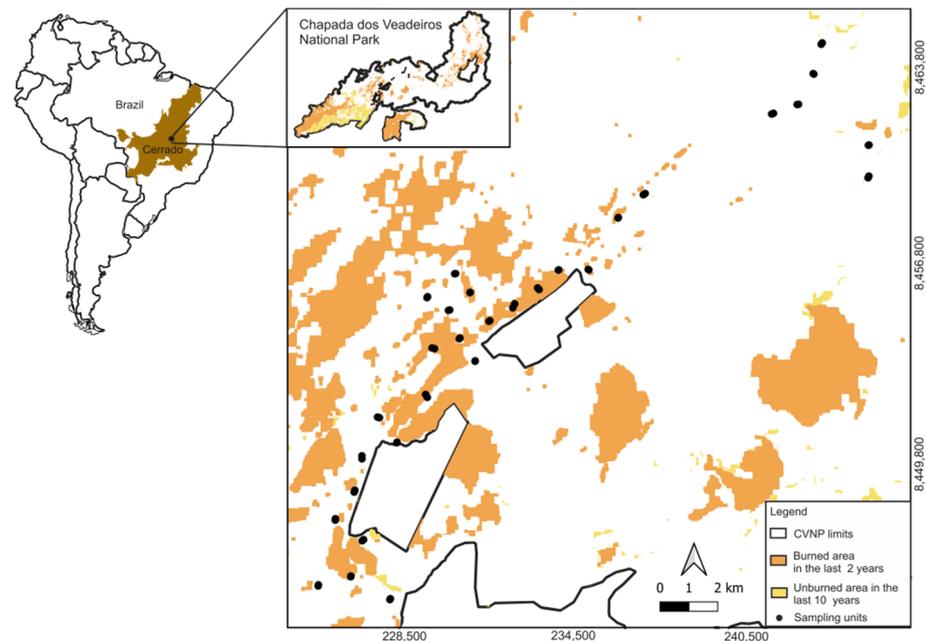


Figure 1. Mammal sampling units' location and spatial distribution of areas recently burned (burned in the last two years before sampling) and long unburned (>10 years without fire occurrence) in the Chapada dos Veadeiros National Park.

The vegetation in CVNP is the Cerrado, a tropical savanna. Cerrado vegetation combines three major formations: grassland, typical savanna, and forest [57]. Grasslands include physiognomies dominated by grasses and herbaceous plants, with some areas showing sparse shrubby vegetation cover but an overall canopy cover of < 5%. Canopy cover is higher in typical savanna formations (5–60%), with continual to sparse grass sublayers. Savanna formations also include palm swamps, a seasonally flooded physiognomy dominated by grasses and herbaceous plants with buriti palm (*Mauritia flexuosa* L. f.) stands. Lastly, forest formations comprise deciduous, semi-deciduous, and evergreen forests (canopy cover 60–95%), including riparian and gallery forests alongside watercourses [57,58]. In this study, we focused on habitat use by mammals in grassland and savanna formations. These vegetation types are more susceptible to fire [59] and dominate the landscape of the region [58]. The fire regime in CVNP is characterized by high fire frequency, with burning occurring mainly at the end of the dry season [60]. The local spatiotemporal configuration of the fire regime is caused by the recurrence of wildfires and prescribed burning [61].

Until recently, the fire exclusion policy was dominant in Brazilian protected areas [62]. However, in 2014 the Integrated Fire Management program (IFM) was implemented in protected savanna areas [61]. In the CVNP, the implementation of the IFM started only in 2017 at fine spatial scales [17]. Based on patch-mosaic burning techniques to create pyrodiversity, the IFM performs prescribed and controlled burns, establishing mosaics with heterogeneous fire regimes. These burns reduce the amount of dry fuel available and help prevent the occurrence of large wildfires and protect fire-sensitive vegetation [61]. In fact, in the protected areas where the IFM has been carried out since 2014, there is a trend toward a decrease in the total area burned and the size of fire scars [17]. Nonetheless,

identifying which burning patterns create suitable habitats for fauna is still an issue to be addressed [61].

The species studied were *Ozotoceros bezoarticus* (pampas deer), two deer species combined (gray deer [*Subulo gouazoubira*] and red brocket deer [*Mazama americana*], hereafter *Mazama* sp.), *Tapirus terrestris* (lowland tapir), and *Chrysocyon brachyurus* (maned wolf). The first four species/groups are herbivores that show different preferences for vegetation types. Pampas deer (mean body mass = 30 kg, ref. [63]) have affinities with grassland and savanna formations [64], *Mazama* sp (brown deer [body mass = 20 kg] and red brocket deer [mean body mass = 30 kg], ref. [65]) prefer forests and forest-open formation transitions areas [66–68], and the lowland tapir (mean body mass = 200 kg, ref. [69]) is associated with forest formations but frequently uses open habitats [70]. Lastly, the maned wolf is the largest canid in South America (mean body mass = 23 kg, ref. [71]), having an omnivorous diet and preying mainly on small-sized mammals [72,73]. Despite *Mazama* sp. being generally described as forest deers, these species may also use open habitats (e.g., typical savanna habitats with some degree of tree cover, as in our study area). Moreover, the number of records of these deer species in our study was considerable, suggesting that open habitats and forest surroundings may be a relevant part of the habitat used by these species. Thus, we included *Mazama* sp. in the analysis to assess a possible effect of the fire regime on the use of open habitats by these deer species. Although the species studied inhabit fire-prone regions, little is known about the effects of fire on habitat use by these animals [74,75].

2.2. Sampling of Medium and Large Mammals

We conducted mammal sampling between February 2020 and April 2021, comprising both dry and wet seasons. We installed a pair of Bushnell® camera traps in 30 fixed sampling units in the CVNP, totaling 60 camera traps installed (Figure 1). All sampling units were located in areas of open vegetation, varying between grassland and savanna formations. We allocated the sampling units along a highway and secondary roads inside the CVNP using a systematic approach [76]. To minimize possible effects of roads on habitat use by mammals, the minimum distance between the camera traps and the road/secondary roads was 300 m. We also established a minimum spacing between sampling units of 1 km to avoid spatial dependence between data. However, some stations were at a distance below this value when necessary (the shortest distance between adjacent stations = 0.82 km). The average minimum distance between adjacent stations was 1.26 km.

We oriented the camera traps of the same sampling unit to different points of the area and adopted a minimum distance of 10 m and a maximum distance of 150 m between them (average distance = 51 m). This variation in camera orientation and distance was necessary for allowing the positioning of the cameras towards distinct water bodies, footprints, trails, feces, or any trace that indicated the passage of mammals, enhancing the probability of mammal recording. Furthermore, we positioned the camera traps 30 cm above the ground, attached to logs or stakes. The settings for the cameras to take photos or videos varied throughout the study. From February 2020 to August 2020 and from December 2020 to April 2021, all cameras were set to take three pictures with each shot, with a 10-s interval between shots. Between September 2020 and November 2020, all cameras were set to record 15-s videos with a one-second shooting interval. All camera traps were configured to be active 24 h per day during the sampling period, regardless of the settings (photo or video). In addition, all stations were sampled simultaneously over 15 months. However, variations in the consumption of battery life and memory card between cameras resulted in unequal effort across sampling units. This difference in sampling effort is not an issue in occupancy modeling since missing observations are implicitly accommodated in the models [77]. We did not use any bait to attract animals.

2.3. Predictor Variables

We evaluated the fire mosaic at three distinct spatial scales, establishing buffers with radii of 50 m, 250 m, and 500 m around camera traps. These buffers represent the multiple spatial scales evaluated in this study (0.8 ha, 19.6 ha, and 78.5 ha, respectively) [78]. We merged the same scale buffers of the camera trap pair of the same sampling unit to obtain a single buffer per sampling unit. For each buffer, we obtained a predictor variable value used in the analysis. Because of the variation in distance between camera traps installed in pairs, buffers did not cover exactly the same amount of area across sampling sites. We tested for any possible effect of this variation in buffer area on the predictor variables values using regression analyses. These analyses did not find any significant effect of the variation in buffer area on the predictor variables (all p -values > 0.05).

We characterized the fire mosaic of the study area using the information on fire scars from 1985 to 2020 (36 years) provided by MapBiomas [60]. The MapBiomas platform uses Landsat satellite images to map fire scars throughout Brazil with a resolution of 30 m. From these fire scar data and using the Quantum GIS software [79], we extracted four variables associated with fire regime: fire frequency diversity, fire age diversity, the proportion of recently burned area (burned in the last two years), and the proportion of long-unburned area (not burned in the last ten years). We acknowledge that there was a fifth variable, which was not accounted for in our analysis. This variable represented the proportion of area burned between 2 and 10 years. The inclusion of this variable, however, would lead to collinearity in predictor variables related to the proportion of areas burned in distinct time intervals. Therefore, we maintained the proportion of recently burned area and the proportion of long-unburned area, not including the area burned in intermediary periods (between 2 and 10 years). We decided to do that because mammal responses to fire may be stronger in the first two years after a fire event [75]. Furthermore, vegetation cover regeneration after a fire occurs mostly in the first year in Cerrado [80]. Thus, including the variable recently burned area allowed us to verify such early responses to fire occurrence. Moreover, we kept the proportion of long-unburned area (>10 years) to evaluate any possible effect of long-term fire suppression on the mammalian communities since fire suppression has been historically implemented in conservation units in Brazil [61].

To obtain predictor variables, we collected information on the years in which fire events occurred for each pixel from the fire scar data and generated two maps containing the frequency and the year since the last fire event for each pixel. We defined fire frequency as the number of years in which a fire scar was present in a given pixel considering the time series from 1985 to 2020. This same time series was used for determining fire age, defined as the number of years since the last occurrence of fire. This occurrence was indicated by the presence of a fire scar in a given pixel. We estimated fire frequency and fire age diversity for each sampling unit and spatial scale (buffer) using the exponential of Shannon H' entropy— $\exp(H')$, which represents the effective number of equally abundant species needed to obtain a given index value [81]. In our estimation of pyrodiversity, instead of species, we estimated the effective number of patches with distinct fire frequencies and fire ages for each sampling unit. We considered the area within the buffers occupied by each fire frequency and fire age as the “abundance” of these fire regimes. We established the proportion of recently burned areas and long-unburned areas in relation to the total buffer area based on the fire age map created. We considered the proportion of the area within the buffer that burned in 2019, 2020, or both as recently burned. For the proportion of long-unburned areas, we considered areas not burned for more than 10 years within the buffer, that is, the last fire event occurred in 2009 or before. We calculated the proportion of recently burned area and long-unburned area for the same scales used for frequency and fire age diversity (0.8 ha, 19.6 ha, and 78.5 ha).

Considering that the detectability of the animals may vary in relation to habitat cover, we evaluated the possible effects of vegetation cover on species detection using the Normalized Difference Vegetation Index (NDVI). This index is related to vegetation characteristics such as canopy structure, biomass, and leaf area [82] and differentiates

the Cerrado formations [83]. In general, higher NDVI values are associated with forest formations, while lower values occur in savanna and grassland formations [83]. To obtain the NDVI, we used satellite images from Landsat 8 for the 2 September 2020 date with a resolution of 30 m. For each sampling unit and each spatial scale, we averaged the pixel values for the NDVI.

We also tested for possible seasonal effects on species detection. For that, we included in the analysis a categorical variable with two levels: dry season and wet season. This division followed the amount of monthly precipitation [56]. Additionally, we tested for any potential bias caused by distinct camera configurations (photographs or videos), including a methodological predictor variable. This method's categorical variable consisted of two levels: photo, in the periods between February 2020 and August 2020 and between December 2020 and April 2021, and video, between September 2020 and November 2020.

2.4. Statistical Analysis

In our study, we established an interval of five consecutive days to consider records of the same species in the same sampling unit as independent. This approach is indicated for occupancy analysis when the studied species have a low population density, larger home range than the sampled sites, and high mobility, which is common for larger mammals [77,84]. For the analyses, we combined the records of two similar deer species *Mazama americana* and *Subulo* (= *Mazama*) *gouazoubira*, in the group *Mazama* sp. By grouping the records, we avoided misidentification as these species are not easily differentiated using camera trap records.

We used single-species, single-season occupancy models to estimate the probability of occupancy (ψ) of sampling units and the probability of detection (p) of large mammal species considering the effect of predictor variables. Occupancy models permit dealing with false absences, i.e., the species is present at the site but has not been detected [85]. Moreover, these models allow the incorporation of predictor variables that may explain the observed variations in the occupancy and detection probabilities of the species [77]. Although the occupancy model assumes that the occurrence of a species in an area does not change within a sampling period, this assumption can be relaxed and the presence/absence of the species is interpreted as use/non-use of a given site [86]. Thus, in our study, the occupancy probability should be interpreted as the "probability of use" of the site. This type of modeling has been widely applied in studies that aim to identify environmental factors affecting the use of different habitats by species, including fire occurrence [87–90].

To investigate the effect of fire regime on occupancy and possible spatial and temporal variations in detectability (Table 1) of species while considering different spatial scales, we structured the occupancy models according to the results of two-step analyses. First, we identified the model structure that best described species detection. For this, we checked the spatial scale of the NDVI effect on detectability and whether the method (photo or video) and seasonality affect the detection of mammals. We created three models which estimated the influence of NDVI on the detection (p) of species at the three distinct spatial scales. We compared the performance of these models according to the Akaike Information Criterion adjusted for small samples (AICc) [91]. The spatial scales represented in the models with good support ($\Delta\text{AICc} < 2$) were used in the following analyses. When more than one spatial scale model presented $\Delta\text{AICc} < 2$ and the NDVI values measured at these scales were correlated (Pearson correlation > 0.5), we used the spatial scale of the model with the lowest ΔAICc (Supplementary Materials Table S1).

Table 1. Predictor variables used in single-species, single-season occupancy models evaluating the effects of vegetation cover, seasonality, and fire mosaic configuration on medium and large-sized mammal space use in Cerrado. We also modeled a potential bias related to different camera trap protocols (photo or video) during the sampling period.

Variable	Type	Multiple Spatial Scales	Description
NDVI	Continuous	Yes	Normalized Difference Vegetation Index indicating the vegetation cover.
season	Categorical	No	Temporal variable representing the two seasons according to mensal precipitation: wet season and dry season.
method	Categorical	No	Variable representing the methods used during the sampling period: photo and video.
div-freq	Continuous	Yes	Fire frequency diversity estimated using the exponential of Shannon entropy. Div-freq values represent the number of effective patches with different fire frequencies needed to obtain the diversity index value.
div-age	Continuous	Yes	Fire age diversity estimated using the exponential of Shannon's diversity index. Div-age values represent the number of effective patches with different fire ages needed to obtain the diversity index value.
burned < 2	Continuous	Yes	Proportion of area burned in the two years before the mammal sampling. Proportion was calculated relative to the total area of the buffer around the camera.
unburned > 10	Continuous	Yes	Proportion of area unburned in the previous 10 years before the mammal sampling. Proportion was calculated relative to the total area of the buffer around the camera.

After defining the appropriate spatial scales, we created models that included the NDVI (in the appropriate spatial scale), seasonality, and method to verify the effect of these variables on species detection (p). These variables were considered isolated or combined in the same model. We also established a model in which detection was constant over time. While we modeled the detection, we kept the occupancy (ψ) varying according to the fire regime variables. This approach avoids possible variations in occupancy from reflecting on detection probability if occupancy is kept constant [77]. To define the variables influencing the detection, we compared the models using the AICc. Variables contained in the models with $\Delta\text{AICc} < 2$ were considered to have high support and were used in the next step of the analyses.

In the second step, we defined the spatial scales for the fire regime variables and their role in occupancy (ψ). Similarly to the approach used for defining the appropriate spatial scale for the effect of the NDVI on detectability, we compared the spatial scales of fire regime variables using AICc-based model selection and selected the spatial scale contained in the model with the lowest ΔAICc . We conducted this comparison for each predictor variable separately. Thus, it was possible for different variables to present distinct spatial scales with better adjustment (lowest ΔAICc) for the same species (Supplementary Materials Table S1). After defining the spatial scale, we assessed the effect of fire frequency diversity, fire age diversity, the proportion of recently burned area, and the proportion of long-unburned area on ψ . For this, we built occupancy models with different combinations of these variables. We also established models considering the effect of the variables alone

and constant ψ . While we modeled the effect of fire on ψ , the detection (p) was modeled according to the results of the first step.

We compared the distinct occupancy models generated using the AICc. When more than one model was supported by the data, we used model averaging to assess the estimates and their respective unconditional standard errors. We included only models with high or medium support ($\Delta\text{AICc} < 4$) in the model averaging [91]. Furthermore, we evaluated the relative importance of the predictor variables by summing the weights of the models in which the variable was present, including only models with $\Delta\text{AICc} < 4$. We excluded from the analyses models that did not converge [88,92].

All predictor variables were standardized (mean = 0; standard deviation = 1) and tested for collinearity using the Variance Inflation Index (VIF). Whenever a variable had $\text{VIF} > 3$ [93], we excluded it from models with other variables. We also checked whether our species records were spatially correlated. Using the Moran Index in the “ape” package [94] for R environment [95], we found no evidence of spatial autocorrelation for any of the variables considered (Supplementary Materials Table S2). Finally, we evaluated whether the data had more variation than assumed by the model with more variables (overdispersion). We use the \hat{c} -value from the goodness-of-fit analysis to determine the presence of overdispersion. All tested models presented \hat{c} -value < 1 ; therefore, we considered our data without overdispersion. All occupancy models were implemented in the “unmarked” package [96] for the R environment.

3. Results

From February 2020 to April 2021, we carried out a sampling effort of 10,112 camera days, obtaining 123 records of pampas deer (*Ozotoceros bezoarticus*), 52 of maned wolf (*Chrysocyon brachyurus*), 29 of brown deer and red deer combined (*Mazama* sp.), and 23 of tapir (*Tapirus terrestris*). All species increased their occurrence when imperfect detection was considered (comparison between naïve occupancy and occupancy probability) (Supplementary Materials Table S3). The pampas deer, the most common species in the study area, occurred in 83% of the sampling units and had the highest occupancy probability. On the other hand, *Mazama* sp. showed the lowest occupancy among the species analyzed in the study area. Individuals in this group were present in 24% of the sample units.

In the study area, pyrodiversity varied between 4.26 and 14.89 for fire frequency diversity and between 1.33 and 8.69 for fire age diversity (78.5-ha scale). This means that the sampling units with the highest pyrodiversity had, in terms of the effective number of patches, around 14 patches with different fire frequencies and 8 patches with different fire ages. The sampling units with lower pyrodiversity have about four patches with different fire frequencies and one patch with a single fire age. The sampling units varied in terms of the proportion of areas that burned in the last two years. For seven sampling units, we did not record fire two years before the mammal sampling. The sampling unit with the highest proportion of recently burned area had 88% of its area affected by fire (scale of 78.5 ha). Of the three sampling units with more than 70% of their total area recently burned, two were subjected to prescribed burning two years before mammal sampling. All sampling units had some part of their area burned in the last 10 years at the 78.5 ha scale while, at the 0.8 ha scale, one unit had not burned in the last 10 years. The sample unit with the highest proportion of unburned area in 10 years had 71% of its area unburned (scale of 78.5 ha).

The NDVI (a proxy for vegetation cover) affected mammal detection probability (p). The model selection indicated an effect of the NDVI on the detection probability of all mammals analyzed. Models containing only the NDVI variable showed $\Delta\text{AICc} < 2$ for all species (Supplementary Materials Table S4). Seasonality (wet or dry seasons) and method (photo or video) apparently did not affect species detectability. Although these variables integrated models with $\Delta\text{AICc} < 2$ (high support), this occurred only when the model also contained the NDVI. Models with the season and method variables alone had negligible support.

Considering the spatial variation in fire regime, *O. bezoarticus* used the space uniformly with little effect of fire-related variables (pyrodiversity and proportion of recently burned or long-unburned areas). The occupancy probability for this species was 90% when considering false absences. Furthermore, the model selection ranked the model with occupancy probability (ψ) constant as the best-supported model (Table 2). This suggests that pampas deer used the space regardless of the spatial configuration of the fire mosaic. Some models containing fire regime variables showed high and medium support ($\Delta AICc < 4$). However, the weighted sum for fire regime variables suggests the low relative importance of these variables on space use by *O. bezoarticus* (weighted sum < 0.35 for all variables; Figure 2a).

Table 2. Occupancy models evaluating the effect of fire regime variables on space use (ψ) by medium and large-sized mammals in Cerrado. Only models with $\Delta AICc < 4$ are shown. K represents the number of parameters in the model, AICcWt and Cum.Wt indicate the relative weight of the model and the accumulated weight, respectively, and $-2LL$ is the log-likelihood. Constant ψ is indicated by “(.)”.

Models	K	AICc	$\Delta AICc$	AICcWt	Cum.Wt	$-2LL$
<i>O. bezoarticus</i>						
$\psi(.)$, p(ndvi)	3	800.75	0	0.22	0.22	-396.91
$\psi(\text{unburned} > 10)$, p(ndvi)	4	801.62	0.87	0.14	0.36	-396.01
$\psi(\text{burned} < 2)$, p(ndvi)	4	801.74	1.00	0.13	0.49	-396.07
$\psi(\text{div-age})$, p(ndvi)	4	802.27	1.52	0.1	0.59	-396.33
$\psi(\text{div-age} + \text{burned} < 2)$, p(ndvi)	5	802.58	1.83	0.09	0.68	-395.04
$\psi(\text{div-freq})$, p(ndvi)	4	803.38	2.63	0.06	0.74	-396.89
$\psi(\text{div-freq} + \text{burned} < 2)$, p(ndvi)	5	803.43	2.68	0.06	0.8	-395.46
$\psi(\text{burned} < 2 + \text{unburned} > 10)$, p(ndvi)	5	803.5	2.75	0.05	0.85	-395.5
$\psi(\text{div-freq} + \text{unburned} > 10)$, p(ndvi)	5	804.3	3.55	0.04	0.89	-395.9
$\psi(\text{div-age} + \text{unburned} > 10)$, p(ndvi)	5	804.42	3.67	0.03	0.92	-395.96
<i>Mazama</i> sp.						
$\psi(.)$, p(ndvi)	3	206.76	0	0.21	0.21	-99.92
$\psi(\text{unburned} > 10)$, p(ndvi)	4	207.03	0.27	0.18	0.39	-98.72
$\psi(\text{div-freq})$, p(ndvi)	4	208.07	1.31	0.11	0.5	-99.24
$\psi(\text{div-last})$, p(ndvi)	4	208.23	1.47	0.1	0.59	-99.32
$\psi(\text{div-freq} + \text{unburned} > 10)$, p(ndvi)	5	208.47	1.71	0.09	0.68	-97.98
$\psi(\text{burned} < 2)$, p(ndvi)	4	208.85	2.09	0.07	0.76	-99.62
$\psi(\text{div-freq} + \text{burned} < 2)$, p(ndvi)	5	209.58	2.81	0.05	0.81	-98.54
$\psi(\text{div-last} + \text{unburned} > 10)$, p(ndvi)	5	209.68	2.92	0.05	0.85	-98.59
$\psi(\text{burned} < 2 + \text{unburned} > 10)$, p(ndvi)	5	209.9	3.13	0.04	0.9	-98.7
$\psi(\text{div-last} + \text{burned} < 2)$, p(ndvi)	5	210.49	3.73	0.03	0.93	-99
<i>C. brachyurus</i>						
$\psi(\text{burned} < 2)$, p(ndvi)	4	429.38	0	0.21	0.21	-209.89
$\psi(\text{div-last} + \text{burned} < 2)$, p(ndvi)	5	429.68	0.3	0.18	0.4	-208.59
$\psi(\text{div-last} + \text{unburned} > 10)$, p(ndvi)	5	430.24	0.86	0.14	0.54	-208.87
$\psi(\text{div-last} + \text{burned} < 2 + \text{unburned} > 10)$, p(ndvi)	6	430.94	1.56	0.1	0.63	-207.64
$\psi(\text{div-freq} + \text{burned} < 2)$, p(ndvi)	5	431.27	1.89	0.08	0.72	-209.39
$\psi(\text{div-last})$, p(ndvi)	4	431.47	2.09	0.08	0.79	-210.93
$\psi(\text{burned} < 2 + \text{unburned} > 10)$, p(ndvi)	5	432.25	2.87	0.05	0.84	-209.87
$\psi(\text{div-freq} + \text{div-last} + \text{burned} < 2)$, p(ndvi)	6	432.78	3.4	0.04	0.88	-208.56
$\psi(.)$, p(ndvi)	3	432.97	3.59	0.04	0.92	-213.02
<i>T. terrestris</i>						
$\psi(\text{div-freq})$, p(ndvi)	4	222.77	0	0.41	0.41	-106.59
$\psi(\text{div-freq} + \text{div-last})$, p(ndvi)	5	223.84	1.06	0.24	0.64	-105.67
$\psi(\text{div-freq} + \text{unburned} > 10)$, p(ndvi)	5	225	2.22	0.13	0.78	-106.25
$\psi(\text{div-freq} + \text{burned} < 2)$, p(ndvi)	5	225.61	2.84	0.1	0.88	-106.56

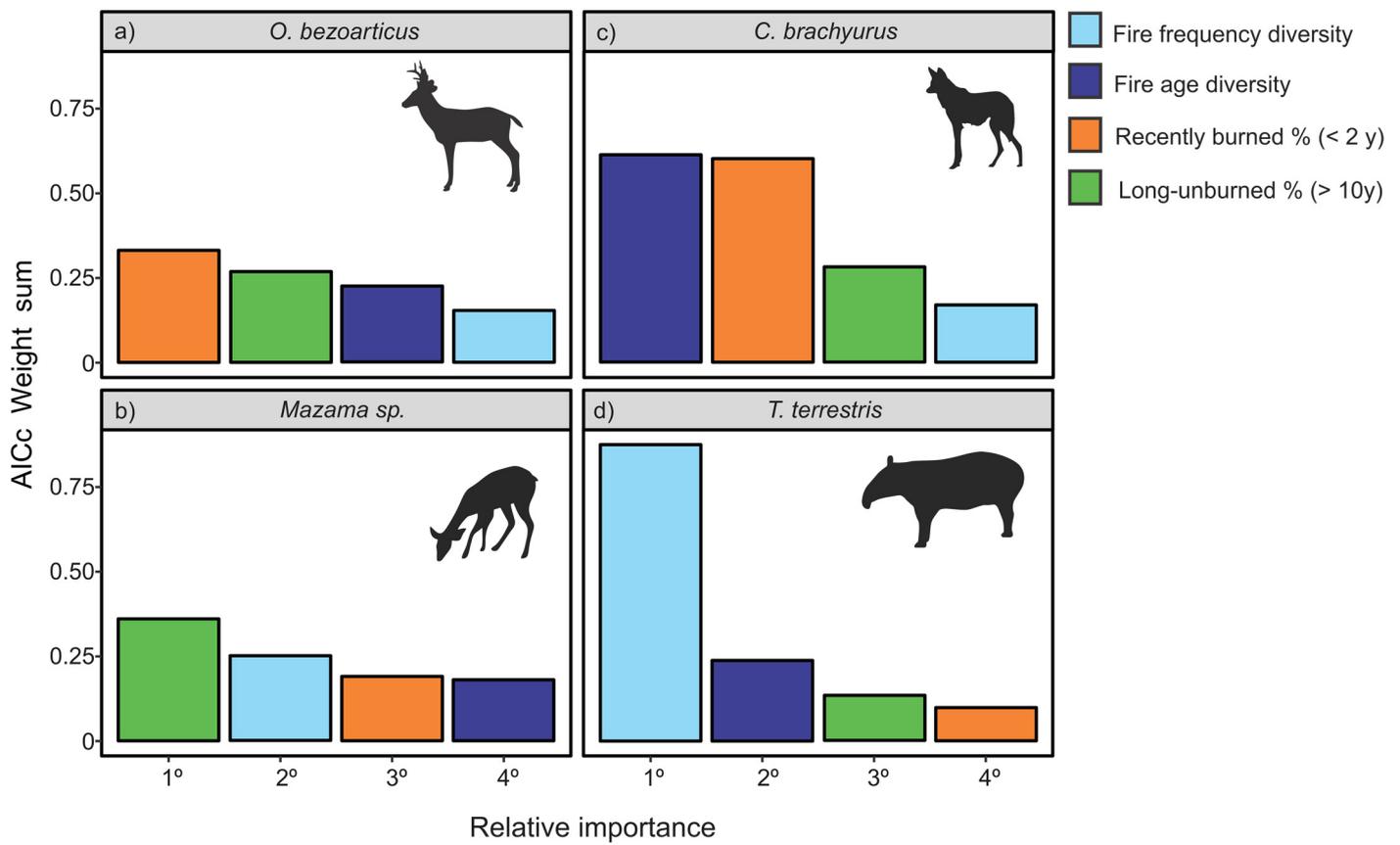


Figure 2. Relative importance of fire regime variables on occupancy probability (interpreted as a proxy for the intensity of habitat use) of *O. bezoarticus* ((a); pampas deer), *Mazama sp.* ((b); brown brocket deer and red brocket deer combined), *C. brachyurus* ((c); maned wolf), and *T. terrestris* ((d); tapir) in the Cerrado. Variable value of importance was calculated as the sum of model weights with $\Delta\text{AICc} < 4$ that included the variable. Fire frequency and fire age diversity were estimated using the exponential of Shannon entropy. The percentage of recently burned area represents the proportion of area burned up to two years before the sampling period and the percentage of long-unburned area represents the proportion of area not burned in the last 10 years before the sampling period. For each species, fire-related variables are ranked in descending order of importance according to their sum of ΔAICc weights.

The other two deer species analyzed together (*Mazama sp.*), were those with the most restricted use of space in the study area. However, the model with constant ψ presented the best rank in model selection (Table 2), suggesting no variation in habitat use across the areas related to spatial variation in the fire regime. Although some models containing fire variables showed medium to high support ($\Delta\text{AICc} < 4$), in general, the relative importance of these variables in the use of space by *Mazama sp.* was low (weight sum < 0.40 for all variables; Figure 2b).

The spatial configuration of the fire mosaic seemed to influence habitat use by the maned wolf *C. brachyurus*. More than half of the sampling units were used by this predator ($\psi = 0.6$), and model selection results indicated several models with medium to high support ($\Delta\text{AICc} < 4$) for the species (Table 2). Fire age diversity and the proportion of area recently burned were the most frequent variables in the models with high support ($\Delta\text{AICc} < 2$). This result is in line with the considerable relative importance of these variables in the use of space by *C. brachyurus* (weighted sum ≥ 0.60 for both fire age diversity and proportion of recently burned area; Figure 2c). Beta estimate values indicated that fire age diversity and the proportion of area recently burned positively affected maned wolf occupancy (Figure 3c). That is, maned wolves used areas where the fire mosaic had a more effective

number of patches with different fire ages and more extensive patch areas burned in the last two years than patches with older fire ages.

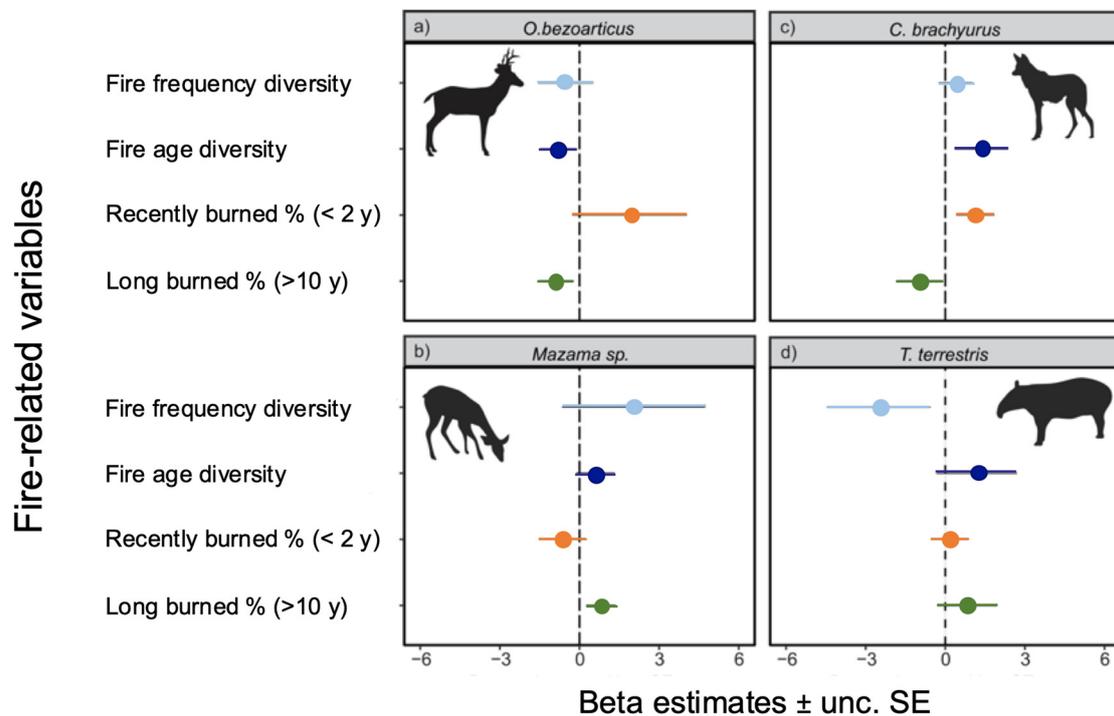


Figure 3. Mean coefficient estimates (β) and unconditional standard errors (unc. SE) for the effect of fire regime variables on occupancy probability (interpreted as the intensity of use) of pampas deer—*O. bezoarticus* (a), brown brocket deer and red brocket deer combined—*Mazama sp.* (b), maned wolf—*C. brachyurus* (c), and tapir—*T. terrestris* (d) in the Cerrado. Fire frequency and fire age diversity were estimated using the exponential of Shannon entropy. The percentage of recently burned area represents the proportion of area burned up to two years before the mammal sampling. The percentage of long-unburned area represents the proportion of area not burned in the last 10 years before the sampling period. β and unc. SE were based on model averaging of models with $\Delta\text{AICc} < 4$.

The results obtained for the tapir *T. terrestris* indicated that habitat use by this large herbivore was influenced by the spatial configuration of the fire mosaic. This species used half of the sampling units ($\psi = 0.53$), and model selection resulted in four models with medium to high support ($\Delta\text{AICc} < 4$) for occupancy data (Table 2). All of these models included fire frequency diversity. This variable showed high relative importance in the use of space by this species (weighted sum = 0.87; Figure 2d). According to beta estimate values, tapirs responded negatively to fire frequency diversity (Figure 3d). This result suggests the avoidance of pyrodiverse mosaics by tapirs. The other variables showed low relative importance and were present in supported models only when accompanied by fire frequency diversity. Models containing these variables alone had no support.

In general, the spatial scales measured for the same predictor variable were correlated. This pattern was clearer for NDVI, diversity of fire age, the proportion of recently burned areas, and the proportion of long-unburned areas. For these variables, all spatial scales showed a correlation > 0.5 . Thus, to avoid inflating our models, we used only one scale per variable. The NDVI measured at the finest spatial scale (0.8 ha) showed a better fit for the detection data of *O. bezoarticus* and *Mazama sp.* when compared to the NDVI on the broader scales (Supplementary Materials Table S1). Conversely, the broadest spatial scale (78.5 ha) had a better fit describing the relationship between *T. terrestris* detection and NDVI. For *C. brachyurus*, the different spatial scales at which the NDVI was measured had similar support. Except for fire age diversity (*C. brachyurus*, 78.5 ha) and fire frequency

diversity (*T. terrestris*, 19.6 ha), the spatial scales had similar support for explaining the effect of fire regime variables on space used by mammals.

4. Discussion

Medium and large mammals showed species-specific responses to fire-related variables. Pyrodiversity and the proportion of recently burned areas had different roles in the space used (occupancy) by the species. For deer species (*O. bezoarticus* and *Mazama* sp.), these variables had low relative importance on their space use. On the other hand, for *C. brachyurus* occupancy, fire age diversity and the proportion of recently burned areas were important, while for *T. terrestris*, occupancy fire frequency diversity was the most important variable. We observed that vegetation cover affected the detectability of the study species. With few exceptions, different spatial scales had similar support for explaining the effect of fire regime on mammal occupancy.

4.1. Fire Regime and Mammal Occupancy

Fire regime variables had distinct effects on mammal occupancy when corrected for differences in detectability. In relation to space use by the deer species, neither *O. bezoarticus* nor *Mazama* sp. were markedly affected by pyrodiversity, the proportion of recently burned, or the proportion of long-unburned areas. On the other hand, fire-related variables affected space use by *T. terrestris* and *C. brachyurus*. For deer species, the results showed a generalized use of the space but with a more restricted use by *Mazama* sp. than by *O. bezoarticus*. These results are compatible with the study by Prada [74] in the Cerrado, which found that *O. bezoarticus* used recently burned and unburned areas with the same intensity. However, our findings for deer species disagree with comprehensive literature indicating herbivore species preferences for recently burned patches related to better forage quality in these areas [41,42,75,97]. This variation in herbivore responses to fire suggests a context-specific influence of fire regime on habitat use. For example, large herbivores in the African savanna [43] and mule deer in conifer forests [38,98] regulate the use of recently burned areas in response to predator activity. Reid, et al. [44], in turn, suggested that cattle foraging in recently burned areas may displace native herbivores (via competition) to long-unburned patches. In our study area, records of cattle and potential predators like *Puma concolor* and *Panthera onca* [99–101] were rare during our sampling [only one record of *P. concolor*, but see 75]. Thus, it seems unlikely that competition and predation are strongly regulating the use of space by deer species in response to fire in our study area. The results obtained for *O. bezoarticus* and *Mazama* sp. may be related to their feeding habits since these species are browsers, especially in open formations [68,102–104]. Browsing herbivores seem to be less attracted to recently burned patches than grazers [105,106]. This may have driven the generalist response to fire observed for deer species in our study area.

Unlike the other studied herbivore species, *T. terrestris* was strongly affected by the fire regime. Based on the weighted sum of the variables, our results suggest a role of fire frequency diversity in the habitat use by this species. In contrast, the proportion of recently burned areas and the proportion of long-unburned areas had negligible influence on tapir habitat use. This pattern differed from other studies that reported the importance of retaining patches with specific fire ages but with no direct effect of pyrodiversity on fauna. For example, in fire-prone Mallee vegetation, native small mammal abundance increased with the extent of the long-unburned area [107] and reptile occurrence was affected by the extent of long-unburned and recently burned areas [29]. However, fire age diversity had no effect on these species. For tapirs, differently from our expectations, the effect of fire frequency diversity on occupancy was negative, which indicates less use of areas with higher pyrodiversity. Negative effects of pyrodiversity on the abundance and occupancy of mammal species have already been reported [30,108] but not for large herbivores. For this group, available studies indicate that pyrodiverse areas provide advantages by offering more foraging opportunities [34,35]. Specifically for tapir populations, the indirect effects

of fire are poorly known, and the scarce available information is based on single fire events [74].

The negative effect of fire frequency diversity on *T. terrestris* suggests that this species may be strongly associated with areas with a given fire frequency regime. Such association was demonstrated for large herbivores in the African savanna where species selected unburned areas or areas with annual or triennial burns [43]. Areas that burn frequently experience reduced vegetation complexity [10], facilitating animal movement between habitat patches [54]. This can be particularly advantageous for *T. terrestris*, which travels long distances and has large home ranges [70,109]. For example, habitat use by *T. terrestris* was reported to be associated with the presence of water bodies [110] and the distribution of food resources [111]. In our study area, gallery forests and palm swamps are important sources of water and fruits present in the diet of tapirs [111–113], but these habitat types occur in low proportions when compared to other Cerrado formations [58]. *Tapirus terrestris* may prefer to use the structurally simplified vegetation of frequently burned areas to move between gallery forests and palm swamps and access such resources. Such areas simplified by fire may be underrepresented in highly pyrodiverse mosaics, leading to negative effects of pyrodiversity [29]. The intense use of areas burned up to one year before in the CVNP reported by [75] provides support for this suggested preference for specific fire regimes by tapirs but see [74].

Less structured vegetation is also found in recently burned areas [114,115] and may attract cursorial predators because of the easier movement in the simplified vegetation after fire [38]. This may explain the importance and the positive effect of the proportion of recently burned areas on the space used by *C. brachyurus* in our study. Our results confirm previous studies that found an association between recently burned areas and predator species, including the maned wolf [40,75,116,117]. This canid can be considered a cursorial predator [118] that preys mainly on small mammals in open areas [72,119,120]. This type of prey may increase in abundance [121] or be more exposed to predation after fire [122]. Conversely, ambush predators of large prey, such as lions, may prefer unburned areas because of the reduced hunting success in low-cover vegetation of recently burned areas [37]. We suggest that the type of hunting strategy of *C. brachyurus* associated with higher predation success in recently burned areas may have led this species to use recently burned areas (up to two years before) more intensively than areas with other fire histories.

In addition to the proportion of recently burned areas, space use by maned wolves was affected by pyrodiversity. The diversity of the fire age was important in determining how this species used the fire mosaic. As we expected, fire age diversity positively affected maned wolf occupancy. This result corroborates previous studies that evaluated the influence of fire age diversity on mammals and other vertebrates in different fire-prone ecosystems [25,27,30,123]. However, there is also evidence for these groups responding negatively or absence of response to pyrodiversity [29,49,124–128]. Pyrodiversity may be advantageous for species when individuals use the resources offered by the different patches of the fire mosaic in a complementary way [25,27,54,129]. This is potentially important for *C. brachyurus*, which has large average home ranges (between 3300 ha and 6700 ha) [130,131] and a generalist diet [119,132]. Furthermore, this species tends to hunt in open vegetation and rest under a dense layer of tall grasses [133,134]. More open and sparse vegetation can be found in recently burned areas, while the presence of denser and taller vegetation is associated with later post-fire successional stages [80,134]. Thus, areas formed by a diversified mosaic of patches at different ages since the last burning can provide favorable environments for the multiple activities of *C. brachyurus*.

4.2. Spatial Scales

Predictor variables influenced mammal space use at different spatial scales. Radford, et al. [49] observed multiple spatial scales associated with the effects of fire on mammal abundance in a savanna. The authors found that the proportion of recently burned areas was relevant at local and landscape scales (0.25 ha to 31400 ha) but with more evident

effects of pyrodiversity detected at the local scale (2800 ha). Our results reinforce the importance of fire's influence on local ecological processes that regulate the mammalian population and community dynamics in fire-prone ecosystems [12,25,33,135,136]. In our study area, the proportion of recently burned areas and the diversity of fire ages seem to affect microhabitat use [51,137] for foraging, hunting, movement between habitat patches, and resting.

For most predictor variables here analyzed, we identified multiple spatial scales with similar importance (evaluated by AICc comparison). The exceptions were the 78.5-ha scale for the relationship between fire age diversity and *C. brachyurus* occupancy and the 19.6-ha scale for the relationship between fire frequency diversity and *T. terrestris* occupancy. Holland and Yang [138] argue that the lack of a marked scale of effect may result from relationships that are not biologically important or because relationships occur at multiple spatial scales. The first case seems to have occurred in our study. We identified the scale of the effect of the variables that were important in explaining the effects of fire on the two species (*C. brachyurus* and *T. terrestris*). We did not find a clear scale of effect, however, when fire regime variables were not important to explain space use by species.

We limited the spatial scale of our study (maximum = 78.5 ha) to avoid spatial dependence between sampling units. Jackson and Fahrig [139] recommend the evaluation of spatial scales ranging from areas smaller than the home range of the species to nine times its average dispersal distance. In fact, the effect of fire on mammals was observed for finer scales (≤ 1 ha) and much larger than the home range of the analyzed species (> 31400 ha) [25,49]. For the species that we studied, the mean home range varies between 120 ha (*Mazama* sp.) and 6700 ha (*C. brachyurus*) [64,66,70,130], and the dispersion distance is expected to be much larger [140]. If the fire variables analyzed in our study affect the home range of species, for example, such an effect may not emerge at finer spatial scales. Thus, we cannot discard the possibility that some responses were not detected because the spatial scale associated with them was larger than the spatial scales we analyzed. Nevertheless, we detected relevant effects of fire regime on space used by mammals within the spatial scale range that we considered (0.8 to 78.5 ha).

4.3. Implications for Fire Management

In fire-prone ecosystems, the idea that heterogeneous fire mosaics are associated with higher biodiversity has encouraged the establishment of pyrodiverse landscapes through prescribed burning [17,21,23,61,141]. However, this approach is subject to criticism due to the mixed support for the hypothesis "pyrodiversity begets biodiversity" [22,28,107]. Complex mosaics with maximum pyrodiversity are not always necessary to enable biodiversity [126,142]. Area extent with a specific fire age may be more relevant for animal populations and communities than highly pyrodiverse mosaics [20,31,49,143]. Here, we demonstrate that both pyrodiversity and the proportion of recently burned areas are important predictors of space use by some medium and large mammals. Our results indicated that fire management targeting specific mammal species should not necessarily establish a highly pyrodiverse landscape. Instead, we suggest that fire management aiming to create heterogeneous mosaics that balance the proportion of recently burned, middle-aged burned, and long-unburned areas, without focusing only on a maximum pyrodiversity value, could also be appropriate. Specifically, we suggest that fire management strategies should maintain large areas burned in the last two years, which could favor species associated with early successional post-fire stages. However, as some species can use multiple patches with different fire ages, it is also necessary to retain a mosaic of patches representing other fire age classes. This approach may be more viable from a logistical and biological point of view. The logistic advantage comes because it eliminates the complexity of planning and executing prescribed burns targeting highly pyrodiverse mosaics. Biological advantage comes because this approach can be suitable for several species and avoid the negative effects that a high pyrodiversity can have on some species, as we observed for tapirs in our study area. Furthermore, other faunal groups, such as birds, reptiles, and invertebrates show species-specific responses to fire [27,29,128], which may differ from the responses observed for

mammals in our study. Thus, it is important to consider this between-group faunal response variation in fire management planning.

Our results demonstrated that the relationship between fauna and fire regime depends on the species studied [27,30], the spatial scale analyzed [125,144], and how the fire regime is characterized [145]. These findings are particularly relevant because they contribute to reducing gaps related to species-specific responses to fire, multi-scale fire effects, and the importance of evaluating multiple fire metrics [146]. In general, pyrodiversity and proportion of recently burned areas were important in determining habitat use by medium and large mammals, at least for tapirs and maned wolves. On the other hand, the proportion of long-unburned areas had negligible influence on mammals. Specifically, our results indicated that maned wolves more frequently use fire mosaics composed of multiple fire ages at the 78.5-ha scale. Moreover, at the 19.6-ha scale, this species made intense use of areas burned up to two years ago. For *T. terrestris*, our findings pointed out that fire mosaics at this same scale (19.6 ha) combining patches with a few different fire frequencies are more frequently used. In contrast, habitat use by deer species seemed to be less affected by variation in fire regime, probably because of their feeding habits. We recommend that the establishment of fire mosaics for conservation purposes be context-specific [19] and species-specific. In addition, fire management strategies that combine “patch mosaic burning” with the maintenance of specific fire-age habitat patches may be a better approach to deal with particular species requirements. Finally, we highlight that even when conducted at fine spatial scales, fire management may influence the habitat used by medium and large-sized neotropical species.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/fire6030110/s1>, Table S1. Model selection evaluating the effect of spatial scale on medium and large-sized mammal detection (p) in Cerrado. K represents the number of parameters in the model, AICcWt and Cum.Wt indicate the relative weight of the model and the accumulated weight, respectively, and -2LL is the log-likelihood. Numbers 50, 250, and 500 represent the spatial scales in which the variables were measured. Spatial scales used in the analysis are in bold. Occupancy (Ψ) was fitted using the fire regime variables at 250-m scale (div-freq + div-age + burned<2 + unburned>10, indicated as “fire regime”) for the NDVI spatial scale analysis. To compare the spatial scales of fire-related variables for ψ , we fitted detection (p) using NDVI at the spatial scale previously selected.; Table S2. Results for the spatial autocorrelation test using Moran’s Index (I). Iobs and Iexp represent observed and expected Moran’s Index, respectively. If the *p*-value is > 0.05, the null hypothesis of no correlation between sampling units is accepted. Table S3. Number of records (detections), number of sampling sites with detections, naïve occupancy, estimated detection probability (p), estimated occupancy probability (ψ), and relative abundance of large-sized mammals of a Neotropical savanna. Detection and occupancy probability and standard deviation estimated by model averaging of models with $\Delta AICc < 4$; Table S4. The model selection used to evaluate the effect of NDVI, season (wet or dry), and method (photo or video) on medium and large-sized mammals detection (p) in Cerrado. K represents the number of parameters in the model, AICcWt and Cum.Wt indicate the relative weight of the model and the accumulated weight, respectively, and -2LL is the log-likelihood. Occupancy (Ψ) was fitted using the fire regime variables (div-freq + div-age + burned < 2 + unburned > 10).

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Informed Consent Statement: Not applicable.

Data Availability Statement: The data that support the findings of this study are available upon reasonable request from the corresponding author [C.V.S.].

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