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AMANDA GOMES DOS ANJOS

A INFLUÊNCIA DO REGIME DE FOGO E DE ASPECTOS DA PAISAGEM SOBRE AS COMUNIDADES DE ANUROS: UMA PERSPECTIVA GLOBAL E LOCAL

ILHÉUS – BAHIA

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Discente: Amanda Gomes dos Anjos

Orientadora: Drª. Maíra Benchimol

Co-orientador: Dr. Mirco Solé

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Drª. Vânia Regina Pivello
Universidade de São Paulo

Dr. Maurício de Almeida Gomes
Universidade Federal de Mato Grosso do Sul

Dr. Pavel Dodonov

Universidade Federal da Bahia

Dr. Diogo Borges Provete

Universidade Federal de Mato Grosso do Sul

Drª. Maíra Benchimol
Universidade Estadual de Santa Cruz
(Orientadora)

É FOGO!

“Onde há fumaça há fogo

E onde houver fogo deve haver atenção

O fogo é quente, muito cuidado

Nunca se aproxime dele não

Fogo na fogueira do acampamento

A dança da chama com o vento

Fogo que aquece nosso alimento

Água e fogo não dão casamento

O fogo do Sol carrega a luz da manhã

Traz um novo dia na alvorada

Onde há fumaça há fogo

E onde houver fogo deve haver atenção

O fogo é quente, muito cuidado

Nunca se aproxime dele não! ”

Mundo Bita

Dedico esta tese aos meus filhos, Maria Clara e João Miguel, a chama mais intensa em meu coração!

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SUMÁRIO

RESUMO

O fogo é um poderoso distúrbio ambiental com a capacidade de moldar diversos ecossistemas em todo o mundo. No entanto, a intensa interferência humana nas últimas décadas nas condições climáticas e no uso e manejo da terra tem provocado drásticas mudanças dos regimes naturais de fogo. Apesar do crescente número de estudos avaliando os efeitos do fogo sobre a biodiversidade, pouco sabemos sobre como as queimadas afetam os anfíbios anuros, os vertebrados mais ameaçados de extinção globalmente e particularmente sensíveis a distúrbios ambientais. Neste contexto, os objetivos dessa tese foram: (i) esclarecer como a anurofauna mundial tem respondido aos regimes de queima naturais e antrópicos; (ii) investigar a influência de características ambientais locais e de paisagem sobre importantes parâmetros do regime de fogo de uma área protegida inflamável do cerrado brasileiro; (iii) avaliar o efeito do regime de fogo da área protegida em questão e demais preditores ambientais sobre a diversidade taxonômica e filogenética das comunidades de anuros. Especificamente, no primeiro capítulo conduzimos uma revisão sistemática da literatura sobre os estudos que avaliaram o efeito das queimadas sobre a abundância, composição, e riqueza de anuros de todo o mundo. Nós demonstramos que não há uma resposta padrão dos anuros ao fogo, uma vez que espécies e comunidades foram afetadas tanto negativamente quanto positivamente pelas queimadas. Além disso, demonstramos que há uma grande lacuna no conhecimento acerca desta temática em ambientes evolutivamente dependentes do fogo, como as savanas tropicais e temperadas. Já no capítulo II, mensuramos a frequência de fogo e o tempo desde o último incêndio no período de 30 anos em 46 paisagens do Parque Nacional da Chapada Diamantina e investigamos a relação entre estes parâmetros do fogo e cinco preditores ambientais considerados importantes determinantes dos regimes de fogo. Encontramos uma grande variação interanual na área total anual queimada no período avaliado. Demonstramos que os tipos de uso e cobertura do solo agricultura, área inundável e Cerrado sentido restrito estão associados com elevadas frequências de fogo. Descobrimos ainda, que a distância ao município mais próximo, a cobertura arbórea e a interação entre cobertura arbórea e altitude foram negativamente relacionados com a frequência de incêndios, enquanto que a superfície de água e a altitude média da paisagem influenciaram positivamente a frequência de incêndios no parque. Comparados aos incêndios mais antigos, os recentes ocorreram em paisagens de altitudes mais baixas e com menor cobertura arbórea. No capítulo III, avaliamos o efeito da frequência de fogo, do tempo desde a última queima e da área total queimada, além de características ambientais em escala local (largura, profundidade e diversidade da margem do corpo d’água) e de paisagem (cobertura arbórea e cobertura de corpo d’água) sobre a diversidade taxonômica e filogenética das comunidades de anuros da Chapada Diamantina. Encontramos que a riqueza taxonômica e filogenética das comunidades de anuros foram determinadas principalmente pela frequência de incêndios e pela cobertura de área queimada, ao passo que a divergência e a estrutura filogenética das comunidades foram melhor explicadas pela cobertura arbórea da paisagem e pela diversidade da margem do corpo d'água local.

Palavras-chave: regime de fogo, manejo de fogo, áreas protegidas, filtragem ambiental, comunidades de anuros, estrutura filogenética.

ABSTRACT

Fire is a powerful environmental disturbance with the ability to shape several ecosystems around the world. However, intense human interference in recent decades in climatic conditions and in land use and management has caused drastic changes in natural fire regimes. Despite the growing number of studies evaluating the effects of fire on biodiversity, little is known about how fires affect anuran amphibians, the most endangered vertebrates globally and particularly sensitive to environmental disturbances. In this context, the objectives of this thesis were to: (i) clarify how the world's frogs have responded to natural and anthropogenic fire regimes; (ii) investigate the influence of local and landscape environmental characteristics on important parameters of the fire regime of a flammable protected area in the Brazilian savanna; (iii) evaluate the combined effects of fire regime in this specific protected area and other environmental predictors on the taxonomic and phylogenetic diversity of anuran communities. Specifically, in the first chapter we conducted a systematic review of the literature on studies that evaluated the effect of fires on the abundance, composition, and richness of frogs worldwide. We revealed there was no clear patterns of response of frogs to fire, as species and communities were affected both negatively and positively by fires. In addition, we demonstrated that there is a large gap in the knowledge about this topic in environments that are evolutionarily dependent on fire, such as tropical and temperate savannas. In Chapter II, we measured the fire frequency and time since the last fire in a 30-year period in 46 landscapes of Chapada Diamantina National Park and investigated the relationship between these fire parameters and five environmental predictors considered important determinants of fire regimes. We found a large interannual variation in the total annual area burned in the evaluated period. We demonstrate that the types of land use and cover agriculture, floodable area and Cerrado sensu stricto are associated with high fire frequencies. We also found that distance to the nearest municipality, tree cover and the interaction between tree cover and altitude were negatively related to the fire frequency, while the water surface and the mean altitude of the landscape positively influenced the fire frequency of the park. Compared to older fires, recent fires have occurred in landscapes at lower altitudes and with less tree cover. In chapter III, we evaluated the effect of fire frequency, time since the last fire and burned area cover, in addition to environmental characteristics at a local scale (width, depth and diversity of the water body margin) and landscape (tree cover and water body cover) on the taxonomic and phylogenetic diversity of anuran communities from Chapada Diamantina. We found that the taxonomic and phylogenetic richness of the anuran communities were mainly determined by the fire frequency and the burned area cover, while the divergence and the phylogenetic structure of the communities were better explained by the tree cover of the landscape and the margin diversity local water body.

Keywords: fire regime, fire management, protected areas, environmental filtration, anuran communities, phylogenetic structure.

INTRODUÇAO GERAL

Nos últimos anos, o fogo tem atraído muita atenção tanto da mídia quanto da comunidade científica, principalmente devido à ocorrência cada vez mais frequente de eventos catastróficos de incêndios em diversas regiões do mundo, como na Indonésia (Chisholm et al., 2016), Estados Unidos (Schoennagel et al., 2017), Canadá (Whitman et al., 2019), Austrália (Ward et al., 2020) e até no Círculo Polar Ártico (Hu et al., 2015). A maior ocorrência de incêndios registrada na América do Sul nos últimos 15 anos ocorreu no Brasil em 2019 (White, 2019). No ano de 2021, identificou-se que aproximadamente 275.000 km² queimaram no Brasil (INPE, 2022), cuja maioria dos focos de fogo foram registrados na Amazônia (40.79%), Cerrado (34.07%) e Mata Atlântica (10.23%). Devido aos graves impactos dos incêndios sobre a fauna e flora e a saúde humana, o fogo é reconhecido como um dos principais desafios do Antropoceno (Malhi et al., 2014; Pyne, 2022). De fato, as modificações dos padrões naturais dos regimes de fogo, desencadeadas principalmente pela intensa interferência humana nas condições climáticas e no uso e manejo da terra (Jolly et al., 2015), podem ser uma grande ameaça à biodiversidade (Kelly et al., 2020). No entanto, o fogo é uma perturbação natural que tem moldado a biodiversidade da Terra por milhões de anos. Diversos ecossistemas, como os campestres e savânicos evoluíram sob a ação periódica de incêndios, nos quais os regimes naturais de fogo desempenham um papel fundamental na determinação da sua estrutura, funcionamento e dinâmica (Bowman et al., 2009). Entende-se por regime de fogo um padrão espaço-temporal de eventos de queima que incorpora importantes parâmetros como a extensão do fogo, estação, frequência, intensidade, severidade (Cochrane & Ryan, 2009). Nos ecossistemas inflamáveis, muitas espécies estão adaptadas a um regime natural particular de fogo e apresentam características de história de vida que lhes conferem resistência a este distúrbio (Bowman et al., 2013; Kelly et al., 2017; Rundel et al., 2018). Assim, o fogo pode atuar como um importante filtro ambiental nestes ecossistemas, selecionando um determinado grupo de espécies com traços fisiológicos, morfológicos e comportamentais associados a uma elevada tolerância às condições ambientais induzidas pelo fogo (He et al., 2019).

Tratando-se da relação evolutiva entre o fogo e os biomas brasileiros, o Cerrado, Pantanal e Pampa podem ser classificados como dependentes da ação do fogo (*fire-dependent*), ao passo que a Amazônia e Mata Atlântica são sensíveis ao fogo (*fire-sensitive*) e a Caatinga é independente deste distúrbio (*fire-independent*) (Pivello et al., 2021). No entanto, todos os biomas contêm tipos de vegetação com diferentes sensibilidades ao fogo (Pivello et al., 2021) e embora a Caatinga seja considerada em amplo aspecto como independente do fogo, ela apresenta regiões que abrigam ecossistemas com distintas sensibilidades a este distúrbio, como a região do Parque Nacional da Chapada Diamantina. O parque é uma área protegida de 152.400 ha, fundada em 1985 e localiza-se no centro da Bahia (41°35' W - 41°15' W; 12°20' S - 12°25' S). É composto por um mosaico de formações vegetais (Fig. 1), incluindo campos ("Campo Limpo" e Campo Rupestre"), savanas ("Campo Sujo" e "Cerrado stricto sensu") e florestas ("Matas ou Floresta Estacional") (ICMBio, 2007).

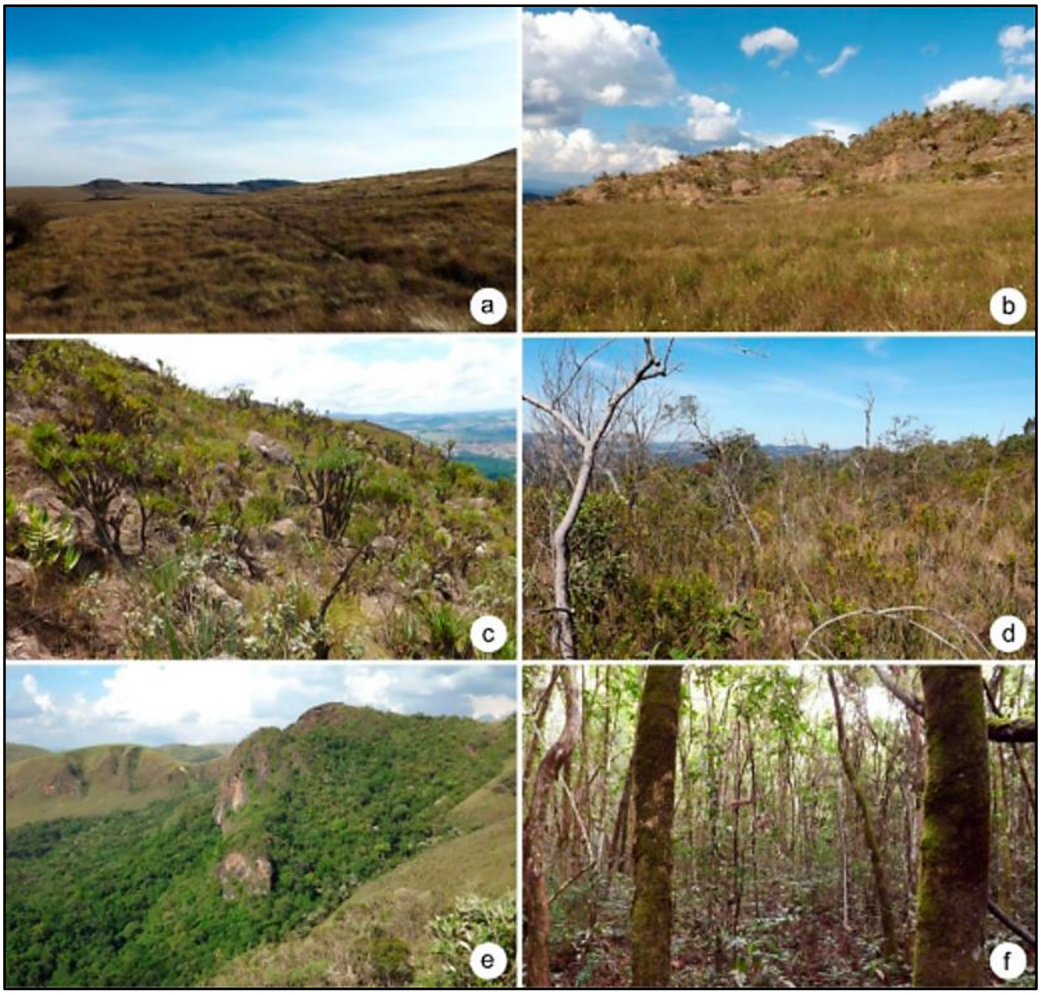

Figura 1. Principais fitofisionomias encontradas no Parque Nacional da Chapada Diamantina: (a) Campo Limpo; (b) Campo Limpo em primeiro plano e ao fundo afloramento rochoso no Campo Rupestre; (c) Campo Rupestre; (d) Cerrado; (e) vista da Floresta Estacional na encosta norte da montanha e (f) interior da Floresta Estacional. Fonte: imagem extraída de Santos et al., 2020.

O PNCD é um ambiente naturalmente propenso ao fogo, devido principalmente à ocorrência de tipos de vegetação altamente inflamáveis (Fig. 2). De fato, eventos de fogo são recorrentes no parque, muitos dos quais são registrados nos topos de montanhas, em locais de difícil acesso (ICMBio, 2007). Sob condições naturais e na ausência de interferência humana, este mosaico de vegetação dependente (como os campestres) e sensível ao fogo (como as machas florestais presentes nos vales do parque) será provavelmente estável e impulsionado principalmente por flutuações climáticas durante longos períodos de tempo (Pivello et al., 2021). No entanto, graves e frequentes episódios de incêndios têm ocorrido no PNCD, como aqueles de 2008 e 2015 (Mesquita et al., 2010) e a fonte destes incêndios é atribuída principalmente às atividades antrópicas (ICMBio, 2007). Embora o fogo seja essencial para a dinâmica de muitos ecossistemas do PNCD, sua ocorrência em locais, estações e frequência inadequadas pode afetar negativamente a fauna e flora desta região (Hu et al., 2018).

Figura 2. Área de Campo Rupestre recentemente atingida pelo fogo (2018). Imagem de Costa, R.N.

Os anfíbios anuros são animais ectotérmicos, apresentam pele permeável, capacidade limitada de dispersão e complexos ciclos de vida e modos reprodutivos associados em menor ou maior grau a ambientes úmidos (Wells, 2007). Essas restrições ecofisiológicas os tornam altamente sensíveis às mudanças das condições abióticas, especialmente de temperatura e umidade (Katzenberger et al., 2012). O fogo pode induzir mudanças pronunciadas nos ecossistemas, alterando principalmente a estrutura da vegetação, condições de umidade e temperatura do solo e parâmetros físico-químicos dos corpos d'água (Lyon et al., 2000). Todas estas modificações afetam diretamente o forrageamento, reprodução e o desenvolvimento dos anuros, e consequemente tornando-os vulneráveis às queimadas. Não obstante, estudos avaliando efeitos do fogo sobre os anuros são escassos (Pastro et al., 2014), especialmente no Brasil (Anjos et al., 2021), cujos diversos biomas tem experimentado severas alterações dos seus regimes de queima (Pivello et al., 2021).

Nos últimos anos, observa-se um crescente esforço científico para avaliar como as atividades humanas tem modificado os habitats naturais dos anuros, investigando as alterações ambientais tanto em escala local quanto de paisagem (Prado & Rossa-Feres, 2014; Almeida-Gomes et al., 2016a). No entanto, a maioria dos estudos se concentra no efeito das atividades antrópicas sobre a riqueza e a composição de espécies, considerando desta forma apenas a diversidade taxonômica, enquanto que as demais facetas da diversidade (como a diversidade funcional e filogenética), ainda são pobremente exploradas (Gumbs et al., 2020). Enquanto a diversidade taxonômica mensura o número de espécies presentes em uma área, a diversidade filogenética incorpora as relações de parentesco entre as espécies (Magurran, 2004). Ao contrário das medidas de diversidade taxonômica, a diversidade filogenética permite uma distinção mais precisa dos papéis ecológicos de cada espécie na comunidade, uma vez que são consideradas como entidades que carregam histórias evolutivas únicas (Pellens & Grandcolas, 2016). Além disso, dado que boa parte das características das espécies tende a ser conservada ao longo das linhagens evolutivas (Harvey & Rambaut, 2000), a diversidade filogenética pode ser um reflexo da diversidade funcional das comunidades. No entanto, esta abordagem deve ser adotada com atenção, tendo em vista que muitos grupos podem divergir funcionalmente apesar de serem filogeneticamente próximos (Srivastava et al., 2012) e neste caso a diversidade filogenética não representa a diversidade funcional em sua totalidade. Assim, a inclusão da diversidade filogenética em estudos ecológicos tem sido progressivamente reconhecida como uma dimensão essencial da diversidade para a conservação da biodiversidade global (Pollock et al., 2017).

Com o intuito de compreender como o regime de fogo afeta os anuros em uma escala global e local, esta tese foi estruturada em três capítulos. No primeiro capítulo realizamos uma revisão sistemática da literatura para elucidar como os anuros são afetados pelo fogo em escala global. Identificamos os padrões de resposta dos anuros tanto aos incêndios naturais quanto aos provocados pelo homem e como os estudos têm sido conduzidos atualmente. No segundo capítulo investigamos como fatores ambientais locais (uso e cobertura predominante do solo e proximidade de assentamentos humanos) e de paisagem (cobertura de copa arbórea, altitude e superfície da água) influenciam o regime de fogo do PNCD, de maneira que pudéssemos compreender em quais cenários os incêndios são mais prováveis de ocorrer e assim poder contribuir com o manejo do fogo nesta área protegida. Por fim, no terceiro capítulo avaliamos o efeito de distintos parâmetros do regime de fogo (frequência de fogo, tempo desde a última queima e área total queimada) e de características ambientais em escala local (largura, profundidade e diversidade da margem do corpo d’água) e de paisagem (cobertura arbórea e de corpo d'água) sobre a diversidade taxonômica e filogenética das comunidades de anuros do parque.

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CAPÍTULO 1

Fire effects on anurans: what we know so far?

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Fire effects on anurans: what we know so far?

Amanda Gomes dos Anjos[1]*, Mirco Solé[2,3] & Maíra Benchimol[2]

[1] *Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, CEP 45662-900, Ilhéus, Bahia, Brazil*

[2] *Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, 45662-900, Ilhéus, Bahia, Brazil*

[3] *Herpetology Section, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany*

Corresponding author: Amanda dos Anjos, Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, CEP 45662-900, Ilhéus, Bahia, Brazil. E-mail: amandaanjos09@gmail.com (A.G. Anjos). Telephone: +55 32 99830-9768

ABSTRACT

Fire is a powerful environmental disturbance with the ability to shape many biomes worldwide. However, global warming, land-use changes and other anthropogenic factors have strongly altered natural fire regimes. Despite the growing number of studies evaluating the effects of fire on biodiversity, little is understood about how burn affects certain groups that are particularly sensitive to climatic extremes, such as anurans. Here, we conducted a global and systematic literature review of studies assessing anurofauna responses to fire disturbances. We used Generalized Linear Mixed-Effects Models and theoretical information criteria to assess how fire affects anuran communities. We analyzed 68 studies, widely distributed in the globe, which examined the fire effects on abundance, richness and/or species behavior. In total, 191 species were considered, being

Gastrophryne carolinensis and *Lithobates catesbeianus* the most evaluated. We reveal a lack of general anurofauna response to fire, as species and communities were either negatively or positively affected by burns. We observed that the fire treatments (Prescribed fire, Wildfire and without fire) and the biome where the study was conducted did not explain the variation in species abundance. Most studies were conducted in biomes classified as Temperate Forests, followed by Tropical Savannas and Tropical Forests. We highlight that future studies should consider factors associated to fire (e.g. fire treatment, fire properties), research design and species biology to explain patterns of species persistence and community structure. Although fire plays a key role in shaping several natural ecosystems, we have recently witnessed drastic changes in natural burning regimes all over the world, which imply leading to severe population reductions and even species extinctions. Given this scenario, government authorities should urgently support and invest in scientific studies that evaluate, monitor and test fire management practices in natural ecosystems and therefore establish mitigation actions to preserve the biota constantly threatened by the imbalance of this environmental disturbance.

Keywords: Amphibians, frog, prescribed fire; review, wildfire

1. Introduction

Fire is a powerful environmental disturbance with the capacity to shape ecosystems and biomes from different regions of the planet (Bowman et al., 2009; He et al., 2019). Vegetations such as Grasslands and Savannas have evolved with the periodic action of natural fires (Bond & Keeley 2005). In these conditions, fire plays a key role in determining the structure, functioning and dynamic of ecosystems, in which multiple animal and plant species have evolved to cope with fire (Brooks et al., 2004). However, recently, many ecosystems have experienced increasingly frequent and intense burning episodes, largely different from their natural fire regimes (Ward et al., 2020).

Human-induced climate changes are among the main factors responsible for global variations in fire regimes (Jolly et al., 2015). In addition, land use and management have played a decisive role in the fire occurrence (Lindenmayer et al., 2020). Catastrophic fire events have been recorded in several regions of the world (Ward et al., 2020). In Brazil, for example, more than 160,000 firespots were recorded in the Atlantic Forest between June 2015 and May 2016, and solely in August 2019, more than 29,944 km² were burned in the Amazon Rainforest (INPE 2019). In tropical forests, many species might be extirpated because they are not pre-adapted to withstand the environmental changes caused by fires, and even low-intensity fires can alter the structure and composition of these ecosystems (Malhi et al., 2014).

In view of their devastating effects, fires are already considered one of the main threats to biodiversity in the Anthropocene (Malhi et al., 2014). Although in the last few decades the number of studies related to the effects of fire on fauna has grown, we still understand little about how organisms respond to fires (Greene et al., 2016). In particular, fauna responses can vary widely. On the one hand, several studies showed negative effects, where burning eliminated habitats and food resources and dramatically changed microclimate conditions in newly burned and adjacent areas (Letnic et al., 2005; Green & Sanecki 2006; Kodandapani et al., 2008). On the other hand, some studies showed that burning exerted positive effects on certain groups, such as increasing the number of opportunistic predators (Geary et al., 2019). Predators are benefited from the greater vulnerability of their prey, which are more exposed in areas where the vegetation has been suppressed by fire (Fuhlendorf et al., 2006; Hutto 2008; Fontaine & Kennedy 2012).

Particularly, anurans have been poorly investigated in the field of fire ecology when compared to other vertebrates (Pastro et al., 2014). These organisms are especially vulnerable to fire because they are ectothermic and almost all aspects of their physiology and behavior are directly affected by the microclimate conditions, such as temperature and humidity (Wells, 2007). In addition to the influence of local temperature on breathing, thermoregulation and metabolism processes, the healthy growth of anuran larvae and post-metamorphic individuals is highly dependent on the temperature of water bodies (Carey and Alexander, 2003). When dealing with behavioral aspects, the local temperature has a considerable influence on the reproductive behavior of frogs. From the early stages of reproduction, such as the choice of vocalization sites, to the final stages where females lay their eggs, water temperature is indeed a key factor (Wells, 2007). Given that fire causes drastic changes on microclimate conditions, as well as on the physical-chemical parameters of water bodies, it can be considered a serious threat to frogs.

In this study, we conducted a comprehensive systematic literature review (1990-2019) on the effects of fire on anurans worldwide, from species to assemblage-level studies. Specifically, our main goals were: (i) to evaluate how anurans species and communities responded to fire disturbance, in terms of positive, negative or neutral responses; (ii) to identify which fire characteristics are decisive in anurofauna responses to this disturbance; (iii) to identify the geographic distribution of studies throughout the world; (iv) to assess the influence of fire incidence and biome type on attributes of anuran communities, especially on abundance of species; and finally (v) to discuss how studies on this topic have been developed so far, providing therefore recommendation for future researches.

2. Methods

2.1. Literature searches

We searched the literature for studies that investigated the anurofauna responses to fire disturbances worldwide, published from 1990 until March 2019. We determined this period because the previously published articles did not meet the selection criteria we used to be included into our database. We searched Web of Science and Google Scholar electronic databases, searching titles, abstracts and keywords, through combinations of the terms “Fire”, “Burn”, “Herpetofauna”, “Amphibian”, “Anuran”, “Frog” and “Toad”. We used the asterisk search operator (*) after the “fire” and “burn” terms to ensure that other similar terms could also be included (e.g. Anuran AND burn*; Anuran AND fire*).

We established three criteria to select the studies to be included in our database. First, we only considered studies with original data, thus excluding publications such as reviews and meta-analyses. Second, the study had to provide the list of evaluated species, even if the focus of the investigation was on species assemblage and/or communities (e.g., Anura, amphibian). As a third criterion, we considered only articles published in indexed journals and therefore did not include academic dissertations and theses. We observed that several studies analyzed the effects of fire combined with other environmental disturbances and considered different groups of herpetofauna. However, we only extracted biological data (at species or assembly level) collected for the fire treatment, and when it came to herpetofauna in general, we used only the primary biological data for anurans.

2.2. Data set

We extracted the following data from each study: (i) geographic location (country, continent and geographic coordinates); (ii) world biome (according to Olson et al., 2001); (iii) experimental design (control-treatment: studies that evaluated the effects in burnt and unburnt areas; treatment: evaluated the effects only in burnt areas; gradient: evaluated the effects considering a burn continuous gradient; before-after-control-treatment: evaluated the effects before and after the burn experiment in both burned and unburned areas; before-after-fire treatment: assessed the effects before and after only in the burned area);

(iv) treatments (control, fire or other disturbances such as logging, herbicide application, thinning, etc.); (v) fire origin (wildfire or prescribed fire); (vi) fire properties (Fire ocorrence; time since last fire, date of fire, frequency, intensity, severity and extent of fire); (vii) level of biological organization study (species or assembly); (viii) biological attributes (abundance, density, richness, diversity, behavior, genetic structure, physio-morphological structure); (ix) species list; (x) sampling design (method and sampling effort); (xi) statistical method used to assess fire effects; (xii) statistical significance and (xiii) study period (short term: ≤ 1 year after the burn; medium term: between 1 to 5 years after the burn; long term: ≥ 5 years).

2.3. Data analysis

To show the regions and biomes in which the studies were conducted, we used QGIS (QGIS Development Team 2019) to create a map based on the Global Classification System for Ecoregions and Terrestrial Biomes produced by the World Wide Fund for Nature (WWF) (Olson et al., 2001). Most of the data extracted from the studies cited in the "Data set" section was used to present an overview of how research on the topic has been developed around the world. Through descriptive statistical techniques (for example, histograms), we identified which biological and fire-related factors have been mostly considered in studies.

To test the hypothesis that fire and the biome affect anurans, we established some criteria to select the studies that would be considered in the statistical models. In order to include only comparable studies, such as those that used the same sampling method and evaluated the same biological attribute (see Fig. 1).

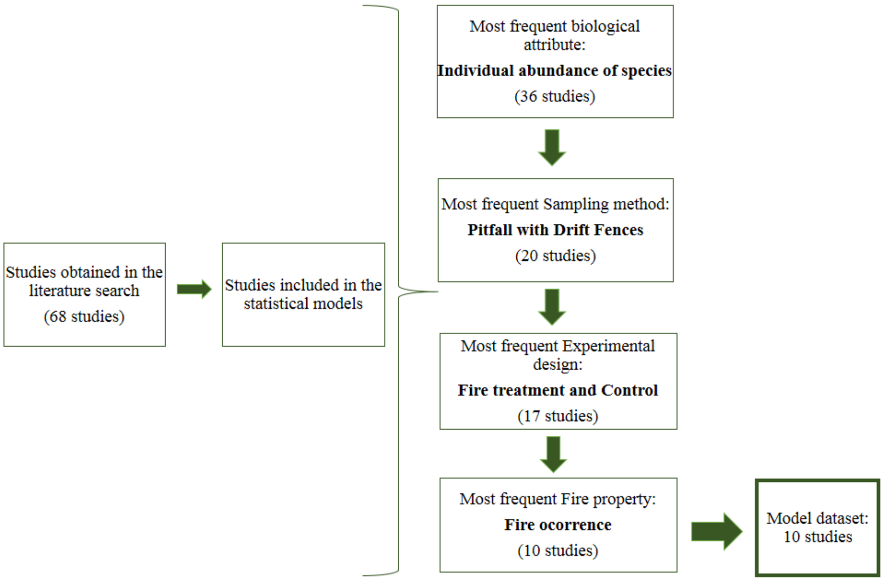

Fig. 1. Criteria used in the selection of studies to be included in the statistical models.

We thus performed Generalized Linear Mixed Effects Models (GLMMs) with the abundance of each species within the assemblage as a response variable and with two predictor variables: Fire Treatment (Prescribed Fire, Wildfire and without fire/Control) and the Biome in which the study was conducted (Temperate Forest, Tropical Forest, Grassland and Savanna). Five models were tested: (1) the null model, which contains only the intercept and considers that the response variable is not dependent on the predictor variables; (2) the full model, in which the abundance of each species is affected by the burn and biome treatment of the study; (3) Fire treatment model, which assumes that the abundance of each species depends only on the fire treatment; (4) the Biome model, which assumes that the abundance of each species is affected only by the biome; (5) interaction model, which assumes that the abundance of each species is influenced by the interaction between the fire treatment and the biome. Given the nature of the response variable (i.e., abundance of each species) and the overdispersion detected in this data (assessed through the overdisp_fun function, see Bolker at al., 2020), we used the Negative Binomial distribution family. Models were run using the *glmer.nb* function of the lme4 package (Bates et al., 2015). We included the ‘study’ as a random factor and the predictor variables were weighted by the 'sampling effort' of each study. To determine which of these predictor variables affect the species abundance, we used the corrected small sample Akaike Information Criterion (AICc), where the best model is indicated by the lowest value of this metric. The analyses were performed in the statistical environment R version 3.6.1 (R Core Team 2019).

3. Results

We obtained 68 studies that analyzed the effect of fire on anurans (Table S1). Of these studies, 24 evaluated species-level effects, whereas all others studied the effects on species communities. Overall, studies evaluated 191 species, being *Gastrophryne carolinensis*, *Lithobates catesbeianus*, *L. sphenocephalus* and *Anaxyrus americanus* the most represented (Fig. S1). Most studies investigated the effects of fire only on abundance of species (23 studies), whereas 15 studies considered only species richness and ten asessed the effects on the behavior of individuals (Fig. 2).

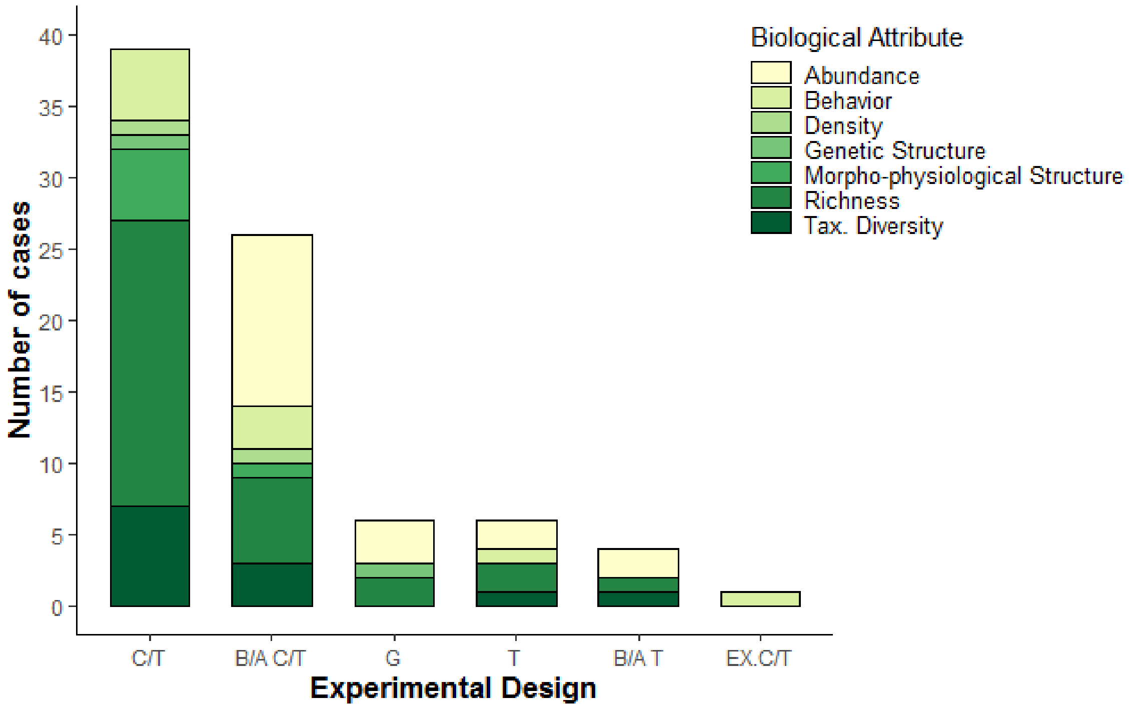

Fig. 2. Number of cases investigating the effects of fire on the different biological attributes of anurans, according to each type of experimental design. C/T: control and fire treatment; B/A C/T: before and after control and fire treatment; G: gradiente of fire; T: Fire treatment; B/A C/T: before and after control and fire treatment; Ex. C/T: experiment control and fire treatment. The number of cases may be greater than the number of studies, because some studies have considered multiple biological attributes.

Forty-eight percent of the studies reported significant effects of fire on any of these biological attributes (n = 33, Table 1), in which 18 studies reported negative effects, 14 reported positive effects and a single study found both negative and positive effects. A total of 47% (n=32) of studies did not identify any effect of fire on frogs and three studies only conducted a descriptive analysis of fire action (Table S1).

Table 1. Selected studies that investigated the effects of fire on anuran amphibians. *= studies that observed significant effect, #= studies that analyzed the effect descriptively. Spp=species. Effects= Main significant effects observed by the authors.

Reference	Biological atributes	Effects
*Allingham and Harvey, 2013	richness of anuran assembly	amphibian richness increases as time since last burn increases.
Arkle and Pilliod, 2010	Density of juveniles of the anuran assembly	-
Ashton and Knipps, 2011	richness of the anuran assembly	-
*Brown et al., 2011	abundance of juveniles of two spp	abundance increases in the site after burn (*Anaxyrus houstonensis, Incilius nebulifer*)
Brown et al., 2014	Behavior, Abundance, Richness, Diversity of the anuran assembly	-
Cano and Leynaud, 2009	abundance of two spp	abundance decreases in recently burned sites (*Leptodactylus latrans*, *L. podicipinus*)
Cole et al., 1997	abundance of one spp	-
Constible et al., 2001	abundance of two spp	abundance decreases at burned sites (*Lithobates sylvaticus, Pseudacris triseriata*)
Drummond et al., 2018	richness of the anuran assembly	amphibian richness increases in the site after burning
#Dunham et al., 2007	abundance of juveniles of one spp	-
Engbrecht and Lannoo, 2012	behavior of one spp	-
Fredericksen and Fredericksen, 2002	abundance and richness of the anuran assembly	-

*Giaretta et al., 1999	density of the anuran assembly	density decreases in the burning sites
Gorman et al., 2013	richness of the anuran assembly	-
*Grafe et al., 2002	behavior of one spp	individuals of *Hyperolius nitidulus* reacted to the sound stimulus of burning, directing themselves to areas of dense vegetation
*Greenberg and Waldrop, 2008	abundance of one spp	abundance increase in the burning sites (*Anaxyrus americanus*)
Greenberg et al., 2016	richness of the anuran assembly	
Greenberg et al., 2018	abundance of two spp	
Greenberg et al., 2018	richness of the anuran assembly	
*Grundel et al., 2015	abundance and richness of the anuran assembly	increased amphibian richness as fire frequency increased. However, the abundance of amphibians increased as the time since the last burn increased
*Gucio et al., 2007	behavior of one spp	*Anaxyrus boreas* individuals prefer severely burned areas to unburnt areas
*Hannah et al., 1998	abundance of the anuran assembly	abundance increase in the burning sites
Hossack and Corn, 2007	abundance of the one spp	-
*Hossack et al., 2009	behavior of one spp	physical models that simulated *Anaxyrus boreas* benefited from the increase in their average daily body temperature at the burning sites
*Hossack et al., 2012	behavior of one spp	reduction of occupation of *Rana luteiventris* individuals in the sites after burning
*Hossack et al., 2013a	abundance of one spp	egg masses of *Rana luteiventris* increase according to larger burnt extensions

*Hossack et al., 2013b	morphophysiological structure of two species	reduction of *Batrachochytrium dendrobatidis* infection rate in burning sites (*Anaxyrus boreas*, *Rana luteiventris*)
*Hromada et al., 2018	abundance of one spp	abundance increase of *Lithobates clamitans* in the burning sites
#Humphries and Sisson, 2012	behavior of one spp	-
Iglay et al., 2013	richness of the anuran assembly	-
*Jones et al., 2000	abundance of anuran assembly	abundance decrease in sites treated simultaneously with burning and herbicide
Kennedy et al., 2012	richness and diversity of the anuran assembly	-
Keyser et al., 2004	abundance of one spp	-
Kilpatrick et al., 2004	abundance of the anuran assembly	-
*Kirkland et al., 1996	abundance of one spp	abundance increase of *Anaxyrus americanus* in the burning sites
*Klaus and Noss, 2016	occurrence of species	occurrence of certain species only in burn-treated sites and undestory reduction
Langford et al., 2008	diversity of the anuran assembly	-
Larson et al., 2014	richness of the anuran assembly	
Lemckert et al., 2004	abundance of one spp	-
Litt et al., 2001	Density of the anuran assembly	-
*Lowe et al., 2013	abundance of anuran assembly	abundance increase of *Litoria freycineti*, *L. olongburensis* and *Crinia tinnula* at an intermediate interval since the last burn
Masterson et al., 2008	richness of the anuran assembly	

*Matthews et al., 2010	richness of anuran assembly	richness decrease in sites treated simultaneously with burning and undestory reduction
Mccoy et al., 2013	richness of the anuran assembly	
Mcdonald et al., 2018	abundance and behavior of one spp	-
*Mcleod and Gates, 1998	abundance of anuran assembly	abundance reduction in burning sites
*Mester et al., 2015	richness of anuran assembly	richness increase in recently burned sites
Moseley et al., 2003	Abundance, diversity, and richness of the anuran assembly	
*Noss and Rothermel, 2015	larval survival of one spp	largest number of *Anaxyrus quercicus* survivors in recent burn sites
*Papp and Papp, 2000	abundance of one spp	abundance decrease in sites after burning (*Phyllodytes luteolus*)
Pennman et al., 2006	fisiology of one spp	
Perry et al., 2009	richness of the anuran assembly	-
*Perry et al., 2012	abundance of anuran assembly	abundance increase in recently burned sites
*Pitt et al., 2013	behavior of one spp	*Anaxyrus americanus* toads maintained greater distances from the woody debris in the unburnt site
*Potvin et al., 2017	genetic structure of anuran assembly	reduction in population genetic diversity at sites after burning
Radford and Fairman, 2015	richness of the anuran assembly	-
*Robertson et al., 2017	genetic structure of one spp	increase in effective population size of *Dryophytes femoralis* in recent burn sites
*Rocha et al., 2008	diet of one spp	larger number of prey in the stomach of *Scinax* cf. *alter* in unburnt site

*Rochester et al., 2010	taxonomic diversity of the anuran assembly	reduction of diversity in sites after burning
Ruthven et al., 2008	abundance and diversity of the anuran assembly	-
*Santos et al., 2019	occurrence of one spp	fire contributed significantly to prediction models of occurrence of *Pelophylax ridibundus*
*Schurbon and Fauth, 2003	richness of anuran assembly	species richness increase significantly as time since last burn increased
Smith et al., 2010	abundance and biomass of the anuran assembly	-
Sutton et al., 2013	abundance of one spp	-
Thomas et al., 2013	abundance of the anuran assembly	-
#Vreeland and Tietje, 2002	abundance of the anuran assembly	-
Westgate et al., 2012	richness and funtional traits of the anuran assembly	-
Wilgers and Horne, 2006	diversity of the anuran assembly	-

Most studies had replicates (92%), including at least two treatments or two sample sites. Eighteen studies included in their experimental design treatments related to other environmental disturbances (in synergy or not with fire), such as logging, herbicide application, selective pruning, among others (Table S1). Most of the studies adopted a "Control-Fire Treatment" and "Before-After-Control-Treatment" experimental design (Fig. 3A). We observed that several fire parameters were used (Table S1). Many studies investigated the fire effects by comparing fire treatments with unburn treatments (parameter characterized as "Fire Ocorrence", Fig. 3B). The time since the last burn and burn severity were also the most used fire parameters in the studies (Fig. 3B). In total, 55% of studies evaluated the effects of prescribed fire, 31% of wildfire, and 5% of both fire types. Only three studies did not specify the origin of the burn and one study evaluated the effects through an artificial simulation of the sound of a fire (parameter characterized as "Fire sound", Table S1).

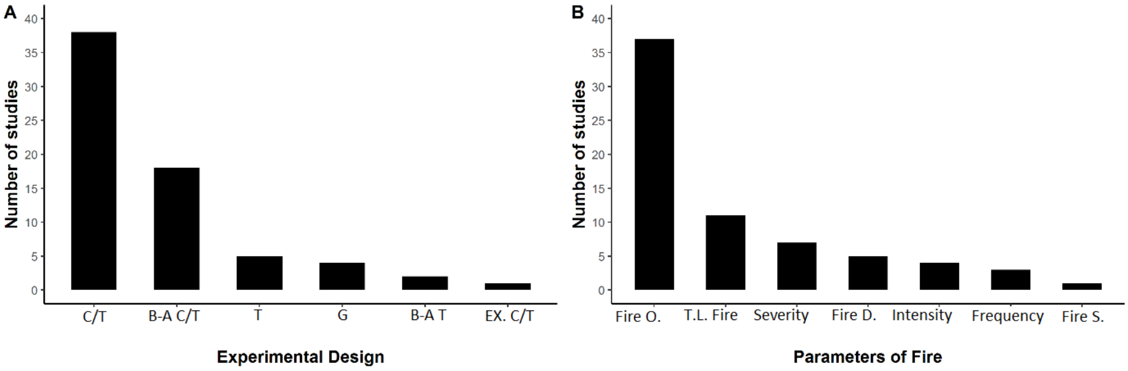

Fig. 3. A: Number of studies that investigated the effects of fire on anurans according to each experimental design. C/T: control and fire treatment; B-A C/T: before and after control and fire treatment; T: Fire treatment; G: gradient of fire; B-A T: before and after fire treatment; Ex. C/T: experiment control and fire treatment. **B:** Number of studies that investigated the effects of different fire properties on anurans. Fire O: Ocorrence of fire;

T.L Fire: Time since last fire; Fire D: studies that know the date the area was burned; Fire S: Artificial simulation of the sound of fire.

The vast majority of studies was conducted in North America (70.5% N=48), followed by South America and Australia (10.2% N=7 each), Africa (5.8% N=4) and Europe (2.9% N=2). These studies are distributed in 12 biomes, of which the four mostly studied were (i) Temperate Forests, (ii) Tropical Fields, Shrubs and Savannas, (iii) Tropical Forests and (iv) Temperate Fields, Shrubs and Savannas (Fig. 4). Studies conducted in Temperate Forests and Flooded Savannas have more frequently reported positive effects of fire on anuran species, while the greatest record of negative effects of fire came from Tropical Forests and Savannas (Fig. 5). Based on the AICc values, we observed that the null model was the best among the other tested models, indicating that the fire treatments and the biome did not influence the abundance of each species in the communities (Table 2).

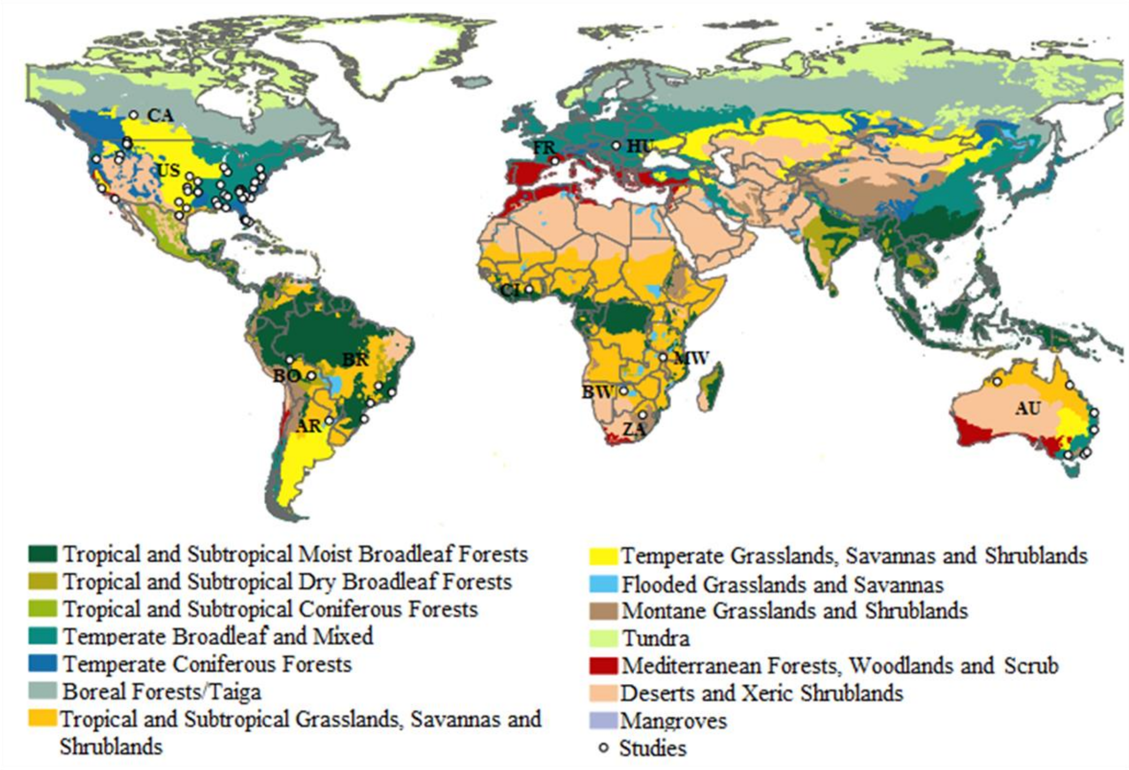

Fig. 4. Geographical locations (white dots) of the 68 studies examined in this study within their respective biome.

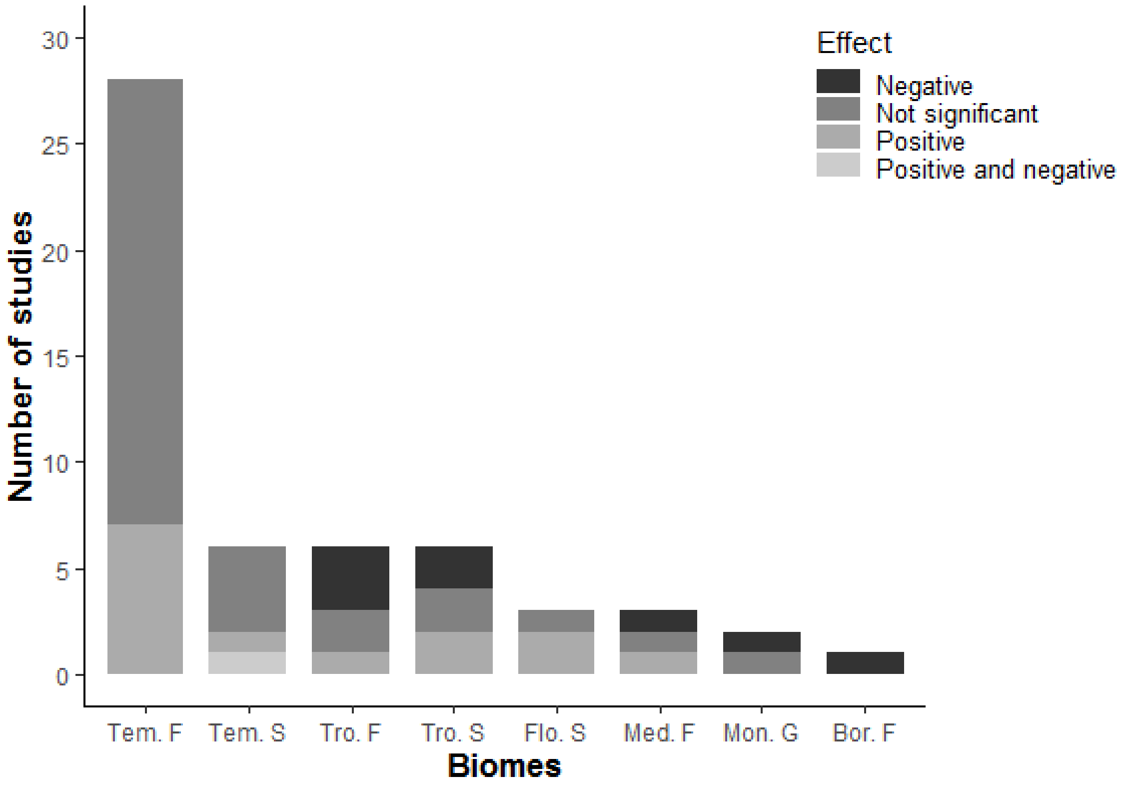

Fig. 5. Number of each type of fire effects on anurans in relation to the biome where the studies were conducted. Tem. F= Temperate forest; Tem. S= Temperate savanna; Tro. F= Tropical forest; Tro. S= Tropical savanna; Flo. S= Flooded savanna; Med. F= Mediterranean forest; Mon. G= Montane grassland; Bor. F= Boreal forest.

Table 2. Results of generalized linear models of mixed effects evaluating the effect of fire and biome treatment on the abundance of each species. Null= contains only the intercept; Full= considers the fire treatment and biome ; Fire treatment= considers only the effect of fire treatment and control (unburned); Biome= considers only the effect of the biome on the abundance of frogs; Interaction= ponders the effect of the interaction between the fire treatment and biome; **AIC$_c$**=Akaike Information Criterion corrected value; **ΔAIC$_c$**=difference in the AICc of the model in question in relation to the model with

lower value of AICc; **d.f**= degrees of freedom; **W**= Akaike weights.

Models	**AICc**	**ΔAIC$_c$**	**d.f**	**W**
Null	645.7	0.0	3	1
Fire treatment	684.2	38.5	5	<0.001
Biome	687.9	42.2	6	<0.001
Full	690.8	45.1	8	<0.001
Interaction (Fire*Biome)	697.8	52.1	12	<0.001

4. Discussion

We synthesize the knowledge on anuran responses to fire at a global scale by revising a data set of 68 studies conducted in various biomes to understand how anuran species and communities have been affected by fire. We showed that 20% of studies reported positive effects of fire on anurans, 26% observed negative effects and 47% of the studies did not detect a significant effect of fire on this group. We observed that the fire treatments and the biome where the studies were conducted failed in explaining the variation on species abundance. However, we emphasize that we performed our analysis with a small set of data, since only studies that measured species abundance using the pitfall trap technique and followed a design of the type 'Control and fire treatment' met the inclusion criteria and were therefore included.

4.1. Anurofauna responses to fire

Fire can induce pronounced changes in environmental ecosystems. Initially, fires alter vegetation, changing the structure of the lower layer and other strata. Sequentially, they cause changes in the microclimate environmental conditions, availability of nutrients in the soil and water bodies (Lyon et al., 2000). These changes in the structure of vegetation can extinguish or create new microhabitats and this can favor or harm biodiversity (Bixbi et al., 2015). Some studies have found an increase in the abundance and species richness of the anuran assembly in burned areas (see Table 1) and several factors are addressed to explain these positive effects (Pilliod et al., 2003). Particularly, one of the main factors is the species adaptation to environments that have historically evolved with the periodic action of burn (Brooks et al., 2004). For example, Brazilian Cerrado has a fauna adapted to surviving through and after fire events (Drummond et al., 2018). During periods when burn is frequent and intense in this ecosystem, anurans usually protect themselves by hiding in shelters, such as burrows (Nomura et al., 2009) and termite mounds (Moreira et al., 2009), in addition to bromeliads and cracks in rocky outcrops (Neves & Conceição 2010). In fact, anuran communities occurring in these types of vegetation that are evolutionarily prone to fire tend to exhibit greater tolerance to fires (Drummond et al., 2018). This pattern has already been reported for other taxonomic groups, such as small mammals, lizards and birds (Briani et al., 2004; Costa et al., 2013; Reis et al., 2016). However, based on the studies included in this review, we did not observe a higher frequency of positive responses from anurans to fire in evolutionarily flammable biomes, possibly due to the low number of studies on this theme carried out in these biomes to date (Figure 5). In addition, generalist species seem to benefit from burning. Here, we note that several studies recorded this scenario with species of the genus Anaxyrus (Table 1), which is widely distributed in the United States and is considered generalist since it occurs in a wide variety of habitats, reproduces in virtually any water body, and has a rapid larval development (AmphibiaWeb, 2019). These traits probably make the species from this genus more resistant to environmental disturbances such as fire (Klaus et al., 2016).

In contrast, the ecological specialization of species can make them more vulnerable to environmental disturbances, as reported for *Phyllodytes luteolus*, a native species from the Brazilian Atlantic coast extremely dependent of bromeliads for survival and reproduction (Papp and Papp, 2000). The authors demonstrated that several characteristics of the bromeliad rosettes suffered alterations after a fire incidence. The microenvironmental modifications of the rosettes that survived, probably, turned them unsuitable for the survival of adult and young individuals of *P. luteolus*, since no individuals from the population were found in this area, where the species was commonly observed before. In general, habitat-specialist species respond differently to environmental disturbances than generalist species (Klaus et al., 2016). Yet studies focused on community structure, such as species richness and taxonomic diversity indices, generally do not consider differences in species composition and therefore hamper the understanding of these divergent responses. We note that a minority of the studies analyzed in this review investigated the effects of fire specifically on each species in the community (Table 1). In some cases, the positive effects of fire observed in certain anuran communities may be the result of the discrepancy between the high abundance of some generalist species to the detriment of the low abundance of specialist species in the burned areas. The marked difference in the abundance values of ecologically distinct (and therefore not comparable) species can be preponderant in the statistical analyses, leading us to erroneous conclusions about the generated results.

4.2. Fire ecology aspects and its influence on fauna responses

In addition to environmental changes caused by fire and species ecological traits, the fauna response variables to this disturbance can also be attributed to factors associated with fire ecology (Pastro et al., 2014). The fire origin (Natural or Prescribed), its parameters (fire surrogates) and temporal variation of fire (fire history) are some of the main factors that should be well understood and considered in research (Kennedy et al., 2009). There is an extensive literature showing that wildfire (e.g., caused by lightning strikes) has an important role in maintaining environmental heterogeneity and biodiversity (Bowman et al., 2009), mainly of the ecosystems that evolved under natural fires with adaptations that give them a greater tolerance to this disturbance (Broks et al., 2004). The prescribed fire (intentional man-made fire) is used worldwide as a tool for forest management, agriculture and biodiversity maintenance (Pastro et al., 2011). However, without planning and a qualified technical team, prescribed burns can cause serious damage to fauna (Loyn & McNabb, 2015). In this review, we did not observe a trend regarding the type of anurofauna response (positive or negative) and fire origin (Natural or Prescribed). However, the fire origin has been previously pointed as one of the main determinants of fire effects on vertebrate diversity (Pastro et al., 2011, 2014).

Most publications on the fire effects on fauna have quantified fire as a binary variable, comparing unburned areas with burned areas (Parr et al., 2003), with 40 studies evaluated herein having investigated anurofauna responses from this perspective (Fig. 5B). However, fire severity (a metric describing the magnitude of how vegetation and soil were altered by burn) is considered the most relevant parameter to examine fire effects on fauna (Kennedy et al., 2009). Studies in which comparisons are made only between burned and unburned areas, when fire severity is heterogeneous, can lead to inconsistent results, such as positive responses of certain species to low severity fire being balanced by negative responses of other species to high severity fire (Smucker at al., 2005). In addition to severity, Kelly and collaborators (2017) demonstrated that models that incorporate more than one parameter to quantify the fire regime (e.g., severity, time since the last fire, Inter-fire interval) are better than those that consider a single metric, because the species' responses burn can vary substantially in relation to the fire properties used.

Fire effects on fauna can be assessed by different ways, but we observed that most of the published literature has been conducted opportunistically in areas that catch fire.

Here, we observed that about 50 studies were conducted in opportunistic occasions, following the “Control and Treatment”, “Treatment” and “Fire Gradient” design (Fig. 3A). Nineteen studies only were conducted considering environmental characteristics before the environment was affected by fire (Fig. 3A). In fact, analyzing the environment structure and conditions before an ecological disturbance occurs is difficult, especially in the cases of wildfire, whose occurrence and frequency are not predictable (Parr et al., 2003). Usually, studies that investigate fauna responses before and after fire are possible because they are conducted with prescribed fire in ecosystems where this activity is routinely practiced for forest management (e.g., Greenberg et al., 2008; Klaus & Noss 2016; Hromada et al., 2018).

Some studies highlighted the importance of assessing fire effects on wildlife from a medium to long-term perspective, since most environmental disturbances and their consequences can evolve over time (Allingham & Harvey 2013). Among the studies that reported negative effects of fire on anurans, three showed immediate effects (Cano & Leynaud 2009; Schurbon & Fauth 2003; Allingham & Harvey 2013). These studies were the only ones found in this review that showed changes in species responses to fire considering the temporal variation. Most studies of anurofuna responses to fire are generally conducted in short and medium term (Minshall et al., 1997; Russell et al., 1999; Radke et al., 2008). Among the 32 studies that did not detect significant effects of fire on anurans, three point out that this scenario is the result of research being conducted in the short term (Kilpatrick et al., 2004; Ruthven et al., 2008; Gorman et al., 2013; Larson et al., 2014), with insufficient duration to accurately assess all the impacts of fires on anurofauna.

4.3. Geographic and ecological distribution of publications

We observed that most publications that investigated anurans responses to fire were carried out in the United States of America (USA), and consequently the most evaluated species are from this region. The larger number of studies conducted in the USA can reflect the prescribed fire activity that is often conducted in their forest ecosystems (Russel et al., 1999). In addition, the high frequency of forest fires that occur mainly in the northern part of this country has triggered significant changes in fire management policies at the state and federal levels. One example is the creation of the National Fire Plan that directs actions and raises financial resources for maintaining fire-adapted ecosystems (Pilliod et al., 2003). The second largest number of publications was observed in Australia, where fires have increased in many ecosystems, particularly those that are historically affected by fire, such as Australian Savannas (Lindenmayer et al., 2011). In fact, this country has been recently subjected to an extensive burn across its territory, indicating that changes to the fire regime have become more frequent and more severe (Nolan et al., 2020). In addition, both countries (USA and Australia) exhibit a strong tradition of research on the ecology of forests and fires, and historically have financially invested in research compared to other parts of the world.

Bases on our review, we noticed that studies on anurofauna responses to fire were mainly originated from studies conducted in forests and savannas from Temperate regions. Additionally, biomes in which fire has an essential role to maintaining vegetation and communities are underrepresented, such as Tropical Savannas (Fig. 4). For example, the Brazilian Cerrado is an evolutionary vegetation dependent on fire and recognized as the savanna retaining the greatest biodiversity in the world (MMA 2019). It was one of the Brazilian vegetations most affected by fires in 2020, when around 6,900 hectares of its area were burned (INPE, 2020). Alternatively, Tropical Forests such as the Amazon

Rainforest and Atlantic Forest evolved independently of the action of fires and, therefore, their fauna and flora do not have adaptations that allow them to cope with this disturbanc (Barlow et al., 2002). However, in recent years, these biomes have also experienced frequent and intense fires of criminal origin (Jolly et al., 2015; National Geographic Society, 2019). Unfortunately, we still have little understanding of how these changes in fire regimes may have affected anuran communities in these biomes.

5. Conclusions

The compiled information in this review improves our understanding of how anuran species and communities have responded to fire, an ecological disturbance that has been dramatically increased due to human activities (Bowman et al., 2009). We observed that anurans can respond both positively and negatively to fire and that these responses can be a result of several factors, such as the ecological singularities of species, fire characteristics and the experimental research design. We emphasize that there is a great gap in the knowledge of how fires affect anurofauna in environments evolutionarily dependent on fire (for example, tropical and temperate savannas), whose natural fire regimes have been drastically modified by human activities in recent years.

In order to avoid erroneous conclusions regarding the anurofauna's responses to fire disturbance, we recommend that further studies consider, whenever possible, an experimental design of the ‘Before and After’ of burn treatment to understand the prior situation of communities and environmental conditions. In addition, research should be conducted in the medium to long-term to ensure that impacts of fire can be detected. It is also important to consider the burn severity as a metric for quantifying fire, considering that this is so far the best parameter to measure changes in vegetation caused by this disturbance (Kennedy et al., 2009). Finally, we recommend that the effects of fire should be investigated specifically for each species and that other traits should also be explored, such as its functional characteristics. In view of the increasing and accelerated use of fire to convert natural environments into pastures and agriculture worldwide, studies on the effects and consequences of burn on biodiversity, especially on anuran amphibians that comprise the most vulnerable vertebrates to environmental changes, are extremely important.

Credit authorship contribution statement

A.G. Anjos conducted data acquisition, data analysis, and led the manuscript preparation. A.G. Anjos, M. Soulé and M. Benchimol contributed to the conceptual ideas behind the manuscript and writing.

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SUPPLEMENTARY MATERIAL

Figure S1. Species considered in the studies and the number of cases found for each species.

‘Others’ include species with one case

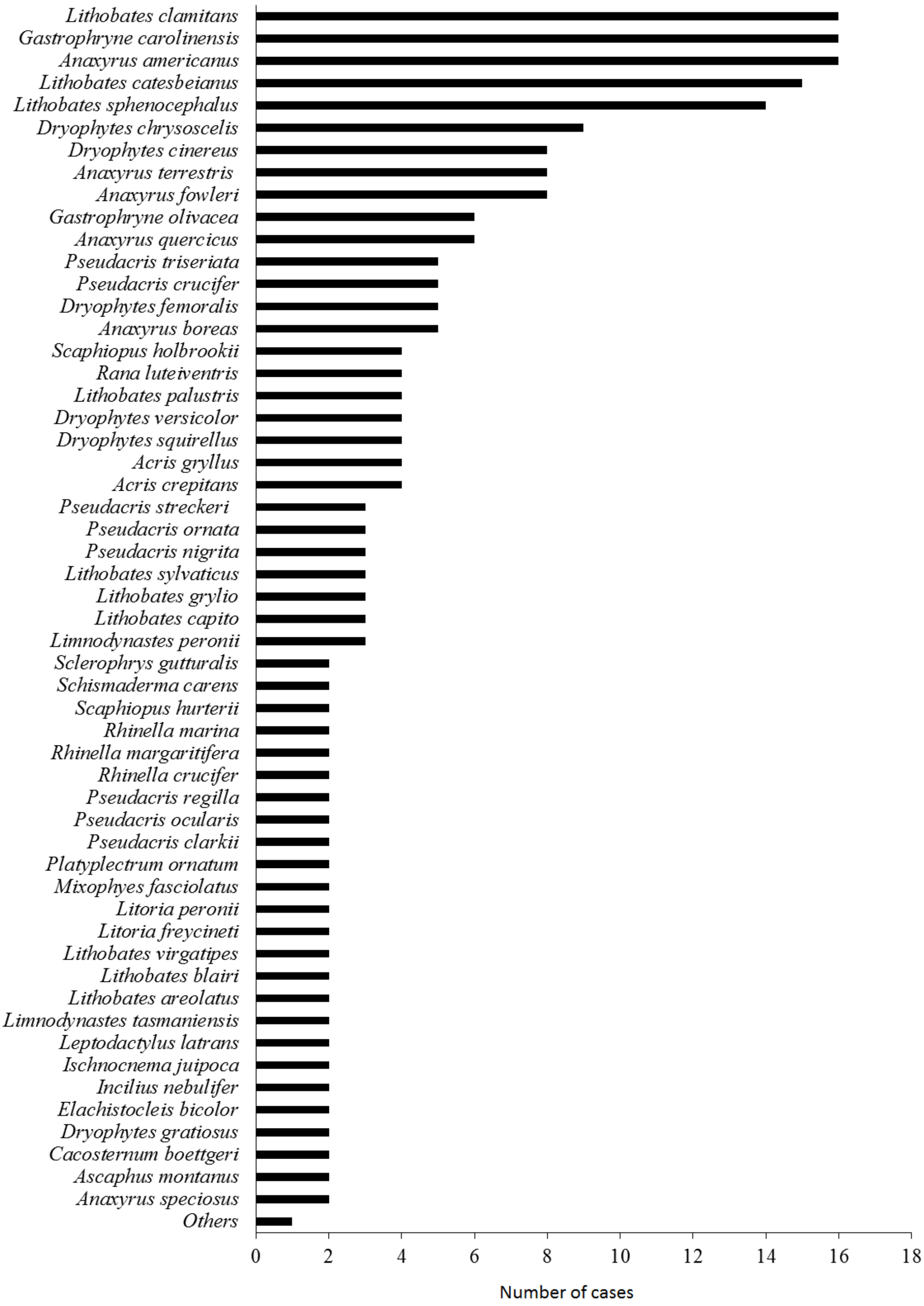

Table S1. Summary of the 68 analyzed publications that evaluated the anuran responses to fire. "Experimental Design": B/A=Before and after, E. =Experimental study; "Fire Origin": P=Prescribed fire, W=Wildfire, U= unknown origin of the burn. Reference: *=studies that observed significant effect, #=studies that analyzed the effect descriptively.

Reference	Journal	Local	Biome	Experimental Design	Treatments	Fire Origin	Fire Parameter	Biological Attribute	Sampling Method
**Allingham and Harvey, 2013* (with leading *)	Current Herpetology	Malawi, Africa	Montane grassland	Control Treatment	Control and Fire	P/W	Date last fire	Abundance, Diversity, Richness	Pitfall with Drift Fences
Arkle and Pilliod, 2010	Forest Ecology and Management	Idaho, EUA	Temperate forest	B/A Control Treatment	Fire	P/W	Severity	Density	Pitfall with Drift Fences
Ashton and Knipps, 2011	Journal of Herpetology	Florida, EUA	Flooded savanna	Gradiente Fire	Fire	W	Frequency	Abundance, Richness	Pitfall with Drift Fences
**Brown et al., 2011*	Journal of Fish and Wildlife Management	Texas, EUA	Temperate savanna	B/A Control Treatment	Control and Fire	P/W	Severity	Abundance, Physio-morphological structure	Pitfall with Drift Fences
Brown et al., 2014	Herpetological Conservation and Biology	Texas, EUA	Temperate savanna	B/A Control Treatment	Control and Fire	W	Fire Ocorrence	Behavior, Abundance, Richness, Diversity	Pitfall with Drift Fences

******Cano and Leynaud, 2009*	European Journal of Wildlife Research	Corrientes, Argentina	Tropical savanna	Control Treatment	Control, Fire and Pasture	P	Date Fire	Abundance, Diversity, Richness	Pitfall with Drift Fences
Cole et al., 1997	The Journal of Wildlife Management	Oregon, EUA	Temperate forest	Control Treatment	Control, Fire/Herbicide, Fire/Logging	W	Fire Ocorrence	Abundance	Pitfall with Drift Fences
**Constible et al., 2001*	Ecoscience	Alberta, Canada	Boreal forest	Control Treatment	Control and Fire	W	Fire Ocorrence	Abundance	Acoustic and visual active search
**Drummond et al., 2018*	Salamandra	Minas Gerais, Brazil	Tropical savanna	B/A Treatment	Fire	W	Fire Ocorrence	Abundance	Acoustic and visual active search
#Dunham et al., 2007	Ecosystems	Idaho, EUA	Xeric shrubland	B/A Control Treatment	Control and Fire	P	Severity	Abundance	Backpack electrofishing
Engbrecht and Lannoo, 2012	Fire Ecology	Indiana, EUA	Temperate forest	Control Treatment	Control and Fire	P	Fire Ocorrence	Behavior	Wildlife cameras
Fredericksen and Fredericksen, 2002	Biodiversity and Conservation	Santa Cruz de La Sierra, Bolivia	Tropical forest	Control Treatment	Control and Fire/Logging	W	Fire Ocorrence	Abundance, Richness	Pitfall with Drift Fences

*_Giaretta et al., 1999_	Biotropica	São Paulo, Brazil	Tropical forest	Control Treatment	Control and Fire	W	Fire Ocorrence	Density	
Gorman et al., 2013	Fire Ecology	Florida, EUA	Temperate forest	B/A Control Treatment	Control, Fire and Fire/Herbicide	P	Date Fire	Richness	Listening station
*_Grafe et al., 2002_	Proc. R. Soc. Lond	Costa do Marfim, Africa	Tropical savanna	E. Control Treatment	Fire	A	Fire Sound	Behavior	Playback
*_Greenberg and Waldrop, 2008_	Forest Ecology and Management	North Carolina, EUA	Temperate forest	B/A Control Treatment	Control, Fire and Fire/Undestoy reduction	P	Iintensity	Abundance, Richness	Pitfall with Drift Fences
Greenberg et al., 2016	Forest Ecology and Management	North Carolina, EUA	Temperate forest	B/A Control Treatment	Control, Fire, Herbicide, Undestory reduction	P	Fire Ocorrence	Abundance, Richness	Pitfall with Drift Fences
Greenberg et al., 2018	The Journal of Wildlife Management	North Carolina, EUA	Temperate forest	B/A Control Treatment	Control, Fire, Fire/Undestory reduction	P	Iintensity	Abundance, Richness	Pitfall with Drift Fences

Greenberg et al., 2018	Forest Ecology and Management	North Carolina, EUA	Temperate forest	Control Treatment	Control, Fire/Dormant season, Fire/Growing season	U	Fire Ocorrence	Richness	Pitfall with Drift Fences
Grundel et al., 2015	Biodiversity and Conservation	Indiana, EUA	Temperate savanna	Gradiente Fire	Scrub/Fire, Savanna/Fire,Grove/Fire, Open forest/Fire, Forest/Fire	U	Frequency	Abundance, Richness	Pitfall with Drift Fences
Guscio et al., 2007	Herpetological Conservation and Biology	Montana, EUA	Temperate forest	Control Treatment	Control and Fire	W	Severity	Behavior	Telemetry radio
**Hannah et al., 1998*	Australian Forestry	Queensland, Australia	Tropical savanna	Control Treatment	Control and Fire	P	Date Fire	Abundance	Pitfall with Drift Fences
Haywood et al., 2004	Applied Herpetology	New South Wales, Australia	Temperate forest	B/A Control Treatment	Control and Fire	P	Fire Ocorrence	Abundance	Acoustic and visual active search
Hossack and Corn, 2007	Ecological Applications	Montana, EUA	Temperate forest	B/A Control Treatment	Control and Fire	W	Date Fire	Behavior	Dip Net
**Hossack et al., 2009*	Forest Ecology and	Montana, EUA	Temperate forest	Control Treatment	Control and Fire	W	Severity	Physio-morphological Structure	Physical models

	Management								
**Hossack et al., 2012*	Conservation Biology	Montana, EUA	Temperate forest	B/A Control Treatment	Control and Fire	W	Severity	Behavior	Dip Net
**Hossack et al., 2013a*	Ecological Applications	Montana, EUA	Temperate forest	Control Treatment	Control and Fire	W	Severity	Abundance	Acoustic and visual active search
**Hossack et al., 2013b*	Biological conservation	Montana, EUA	Temperate forest	Control Treatment	Control and Fire	W	Fire Ocorrence	Physio-morphological Structure	Acoustic and visual active search
**Hromada et al., 2018*	Forest Ecology and Management	Kentucky, EUA	Temperate forest	Control Treatment	Control and Fire	P	Fire Ocorrence	Abundance, Richness	Pitfall with Drift Fences
#Humphries and Sisson, 2012	Journal of Herpetology	North Carolina, EUA	Temperate forest	Treatment	Fire	P	Fire Ocorrence	Behavior	Telemetry radio
Iglay et al., 2013	Wildlife Society Bulletin	Mississipe, EUA	Temperate forest	Control Treatment	Control, Fire, Herbicide, Fire/Herbicide	P	Fire Ocorrence	Richness, Diversity	Pitfall with Drift Fences
**Jones et al., 2000*	Journal of Range	Oklahoma, EUA	Temperate forest	Control Treatment	Control, Fire/Herbicide,	P	Fire Ocorren	Abundance	Pitfall with Drift Fences

	Management				Herbicide		ce		
Kennedy et al., 2012	Check List	Botswana, Africa	Tropical savanna	B/A Treatment	Fire	W	Fire Ocorrence	Abundance, Diversity, Richness	Pitfall with Drift Fences
Keyser et al., 2004	Virginia Journal of Science	Virginia, EUA	Mediterranean forest	B/A Control Treatment	Fire	P	Iintensity	Abundance	Pitfall with Drift Fences
Kilpatrick et al., 2004	Southern Research Station	South Carolina, EUA	Temperate forest	Control Treatment	Control, Fire, Thinning	P	Fire Ocorrence	Abundance	Pitfall with Drift Fences
**Kirkland et al., 1996*	The American Midland Naturalist	Pennsylvania, EUA	Temperate forest	Control Treatment	Control and Fire	W	Fire Ocorrence	Abundance	Pitfall with Drift Fences
**Klaus and Noss, 2016*	The Journal of Wildlife Management	South Carolina, EUA	Temperate forest	B/A Control Treatment	Control, Fire and Fire/Undestory reduction	P	Fire Ocorrence	Richness	Funil trap
Langford et al., 2007	Herpetological Conservation and Biology	Mississipe, EUA	Temperate forest	Control Treatment	Control and Fire	P	Fire Ocorrence	Richness, Diversity	Acoustic and visual active search
Larson, 2014	Environmental Management	Missouri, EUA	Temperate savanna	Control Treatment	Control, Fire,	P	Fire Ocorren	Behavior, Abundance, Richness	Acoustic and visual active

					Fire/Pasture		ce		search
Litt et al., 2001	Society for Ecological Restoration	Okaloosa, EUA	Temperate forest	Control Treatment	Control, Fire, Herbicide, Felling	P	Fire Ocorrence	Density	Pitfall with Drift Fences
**Lowe et al., 2013*	International Journal of Wildland Fire	Queensland, Australia	Tropical forest	Gradiente Fire	Fire	W	Date Fire	Abundance	Acoustic and visual active search
Masterson et al., 2008	Applied Herpetology	Gauteng, Africa	Montane grassland	Treatment	Fire	W	Date last fire	Richness	Pitfall with Drift Fences
**Matthews et al., 2010*	Journal of Wildlife Management	North Carolina, EUA	Temperate forest	Control Treatment	Control, Fire and Fire/Undestory reduction	P	Fire Ocorrence	Richness	Pitfall with Drift Fences
Mccoy et al., 2013	Natural Areas Journal	Florida, EUA	Temperate forest	Control Treatment	Control and Fire	P	Date last fire	Richness	Pitfall with Drift Fences
Mcdonald et al., 2018	Forest Ecology and Management	Carolina, EUA	Temperate forest	Control Treatment	Control and Fire	P	Fire Ocorrence	Behavior, Abundance, Physio-morphological structure	Artificial mesocosm
**Mcleod and Gates, 1998*	American Midland Naturalist	Maryland, EUA	Temperate forest	Treatment	Fire, Forest	P	Fire Ocorrence	Abundance	Pitfall with Drift Fences

**Mester et al., 2015*	Biological conservation	Budapest, Hungria	Temperate forest	Control Treatment	Control, Fire, Fire/Pasture, Pasture	P	Date Fire	Richness	Acoustic and visual active search
Moseley et al., 2003	The Southwestern Naturalist	Georgia, EUA	Temperate forest	Control Treatment	Control and Fire	P	Fire Ocorrence	Abundance, Diversity, Richness	Pitfall with Drift Fences
**Noss and Rothermel, 2015*	Journal of Herpetology	Florida, EUA	Flooded savanna	Treatment	Fire	P	Date last fire	Abundance	Natural mesocosm
**Papp and Papp, 2000*	Herpetological Review	Espírito Santo, Brazil	Tropical forest	B/A Control Treatment	Fire	U	Date last fire	Abundance	Acoustic and visual active search
Pennman et al., 2006	Pacific Conservation Biology	New South Wales, Australia	Temperate forest	Control Treatment	Control and Fire	P	Fire Ocorrence	Physio-morphological Structure	Physical models
Perry et al., 2009	Restoration Ecology	Arkansas, EUA	Temperate forest	Control Treatment	Control and Fire	P	Fire Ocorrence	Richness	Pitfall with Drift Fences
**Perry et al., 2012*	Forest Ecology and Management	Arkansas, EUA	Temperate forest	Control Treatment	Fire	P	Date last fire	Richness	Pitfall with Drift Fences

*_Pitt et al., 2013_	Forest Ecology and Management	North Carolina, EUA	Temperate forest	Control Treatment	Control and Fire	P	Fire Ocorrence	Behavior	Telemetry radio
*_Potvin et al., 2017_	Journal of Applied Ecology	Victoria, Australia	Temperate forest	Control Treatment	Control and Fire	W	Fire Ocorrence	Genetic structure	Acoustic and visual active search
Radford and Fairman, 2015	Wildlife Research	Kimberle, Australia	Tropical savanna	Control Treatment	Control and Fire	P	Date last fire	Abundance	Funil trap
*_Robertson et al., 2017_	The American Genetic Association	Florida, EUA	Flooded savanna	Gradiente Fire	Fire	W	Iintensity	Genetic structure	-
*_Rocha et al., 2008_	Brazilian Journal Biology	Santa Catarina, Brazil	Tropical forest	Control Treatment	Control and Fire	P	Fire Ocorrence	Physio-morphological Structure	Acoustic and visual active search
*_Rochester et al., 2010_	Journal of Herpetology	California, EUA	Mediterranean forest	B/A Control Treatment	Fire	W	Fire Ocorrence	Diversity	Pitfall with Drift Fences
Ruthven et al., 2008	The Southwestern	Texas, EUA	Temperate savanna	Control Treatment	Control and Fire	P	Fire Ocorren	Abundance	Pitfall with Drift Fences

	Naturalist						ce		
**Santos et al., 2019*	Biological Journal of the Linnean Society	Collobrieres, França	Mediterranean forest	Control Treatment	Fire	W	Frequency	Abundance	Occurrence record
**Schurbon and Fauth, 2003*	Conservation Biology	South Carolina, EUA	Temperate forest	Control Treatment	Control and Fire	P	Date last fire	Richness, Diversity	Pitfall with Drift Fences
Smith and Rissler, 2010	Restoration Ecology	Alabama, EUA	Temperate forest	Treatment	Fire	P	Date last fire	Richness, Diversity	Pitfall with Drift Fences
Sutton et al., 2013	Forest Ecology and Management	Alabama, EUA	Temperate forest	B/A Control Treatment	Control, Fire, Thinning, Fire/Thinning	P	Fire Ocorrence	Abundance, Richness	Pitfall with Drift Fences
Thomas et al., 2013	Herpetological Bulletin	Madre de Dios, Peru	Tropical forest	Control Treatment	Control and Fire	P	Fire Ocorrence	Abundance, Richness	Acoustic and visual active search
#Vreeland and Tietje, 2002	General Technical Report	California, EUA	Mediterranean forest	B/A Control Treatment	Control and Fire	P	Fire Ocorrence	Abundance	Refuge Trap

Westgate et al., 2012	Oikos	New South Wales, Australia	Temperate forest	Control Treatment	Control and Fire	W	Fire Ocorrence	Behavior, Richness	Acoustic and visual active search
Wilgers and Horne, 2006	Journal of Herpetology	Kansas, EUA	Temperate savanna	Control Treatment	Control and Fire	P/W	Date last fire	Diversity	Pitfall with Drift Fences

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CAPÍTULO 2

Patch and landscape features drive fire regime in a Brazilian flammable ecosystem

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Patch and landscape features drive fire regime in a Brazilian flammable ecosystem

Amanda G. Anjos[1*], Swanni T. Alvarado[2,3], Mirco Solé[4,5] and Maíra Benchimol[4]

[1]*Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, CEP 45662-900, Ilhéus, Bahia, Brazil*

[2] *Programa de Pós-graduação em Agricultura e Ambiente, Universidade Estadual do Maranhão, Praça Gonçalves Dias, CEP 65800-000, Balsas, Maranhão, Brazil*

[3]*Programa de Pós-graduação em Geografia, Natureza e Dinâmica do Espaço, Universidade Estadual do Maranhão, Avenida Lourenço Vieira da Silva, Jardim São Cristóvão, CEP 65055-310, São Luís, Maranhão, Brazil*

[4]*Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, 45662-900, Ilhéus, Bahia, Brazil*

[5]*Herpetology Section, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany*

Corresponding author: Amanda G. dos Anjos, Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, CEP 45662-900, Ilhéus, Bahia, Brazil. E-mail: amandaanjos09@gmail.com (Anjos, A. G.). Telephone: +55 32 99830-9768

ABSTRACT

The flammable ecosystems are evolutionary dependent on the periodic action of fire. Several environmental factors, both at local and landscape scales, can affect fire regimes in these ecosystems differently. Here, we evaluated the influence of local and landscape features on two parameters of the fire regime of a flammable protected area of the Brazilian savanna: The Chapada Diamantina National Park. We characterized both fire frequency and the time since the last fire, from 1990 to 2019 and measured five environmental predictors (tree canopy cover, altitude, water surface, predominant land use and distance to the nearest municipality). We used Generalized Additive Models for Location, Scale and Shape (GAMLSS) to assess the influence of environmental predictors on the measured fire regime parameters. We found a large interannual variation in the total annual area burned in the studied period. In total, 68% of the protected area (1,030 km²) was burned at least once and 32% (486 km²) was unaffected by fires during the study period. Predominant land use, distance to the nearest municipality, tree cover and the interaction between tree cover and altitude were negatively related to fire frequency, while the water surface and altitude positively influenced fire frequency in the park. Compared to older fires, recent fires occurred in landscapes at lower altitudes and with lower tree cover. Our results demonstrate that the fire frequency and time since the last fire were highly variable across the park, reflecting the strong influence of landscape heterogeneity on their parameters.

Keywords: Burned area, fire management, land use, protected areas, tree canopy cover

1. Introduction

Fire plays a key ecological role in several terrestrial environments, especially in flammable ecosystems such as shrublands, grasslands and savannas, that evolved under periodic wildfire (Bowman et al., 2009). As a result, the biota is adapted to variation in fire regimes in these ecosystems and many species depend on this process to complete their life cycles (e.g., plant species, see Rundel et al., 2018) or are benefited by habitats or resources availability induced by wildfires (e.g., several faunal species, see Kelly et al., 2017). The fire regime refers to the spatio-temporal integration of individual fire events in a given place, according to their spatial and temporal attributes, magnitude, type of fire and synergy with other disturbances, being influenced by several abiotic and biotic factors (Bowman et al., 2013).

The climate conditions (e.g., temperature and precipitation), topographic characteristics (e.g., altitude and slope) and vegetation features (e.g., net primary productivity or vegetation type) comprise key drivers of fire regimes, given their strong influence in determining the availability and condition of fuel (fuel moisture and distribution) and sources of ignition (lightning) (He et al., 2019). In flammable ecosystems, species are adapted to specific conditions of the fire regime, including a given frequency, intensity, size, season and type of fire (Keeley et al., 2011). Therefore, drastic changes in these components mainly due to human activities can affect the structure and composition of vegetation (Bond and Keeley 2005) and ecosystem functioning (Pausas and Keeley 2019), consequently jeopardizing biodiversity maintenance (Kelly et al., 2020).

The last decades are characterized by the significant role of human activities in the formation and dynamics of terrestrial ecosystems (Kelly et al., 2020). Indeed, the natural patterns of the fire regime have been drastically affected around the world driven by anthropogenic impacts (Bowman et al., 2020; Lindenmayer et al., 2020). For instance, the increasing emissions of greenhouse gases mainly due to land use and cover changes and burning of fossil fuels are inducing to global warming and turning natural environments more susceptible to wildfires (Bowman et al., 2009). In addition, several fire-dependent environments have been experiencing larger, more severe and more frequent fires due to climate change (Moreira et al., 2020; Oliveira et al., 2021; Ward et al., 2020). Human influence in fire regime has also been documented within protected areas (Alvarado et al., 2018), which are widely recognized as essential instruments to promote nature conservation, as they maintain the integrity of habitats, species diversity and ecosystem health (Mansuy et al., 2019). Therefore, understanding the main drivers of fire regimes within protected areas is crucial to propose effective management actions to both prevent and control fires.

Some studies have revealed that topographic features, such as altitude, can facilitate or hinder the spread of fire, contributing to a greater or lesser fire frequency in a given area (Cyr et al., 2007; Mansuy et al., 2019; Probert et al., 2019). In fact, topographically complex landscapes (i.e., with large altimetric variation) can show wide variation in the fire frequency (Probert et al., 2019). Also, vegetation structure can directly affect the amount of fuel available to burn in the landscape (He at al., 2019). Thus, landscapes composed by high vegetation heterogeneity tend to present a high variation in the availability of biomass, affecting the frequency, intensity and severity of fires (He at al., 2019). Although several environmental factors inducing to spatial heterogeneity of fire regimes are recognized, the current knowledge of their influence is essentially based on studies performed at the local level (Moreno and Chuvieco 2016; Peeler and Smithwick 2021), which can limit the understanding of the impact of fire on ecosystems. It is essential to address this issue at the landscape context, so that the effects of environmental factors on components of fire regimes should be incorporated into studies and, therefore, contribute in improving fire management practices for the conservation of flammable ecosystems (Bélisle et al., 2016; Peeler and Smithwick 2021).

Here, we analyzed the spatio-temporal patterns of fire regime in a flammable protected area of the Brazilian savannah – the Chapada Diamantina National Park (CDNP). We assessed the influence of five local and landscape features on two essential parameters of fire regime (fire frequency and time since the last fire), aiming to reveal which drivers explain the spatial variation of both fire parameters in contrasting landscapes within the CDNP. We hypothesized that fire frequency and the time since the last fire are not randomly distributed across the park, as patch and landscape-scale features are modulating these patterns. Specifically, we predict that fire frequency will be higher in landscapes (i) composed of more rugged relief, considering that the probability of lightning occurrence is higher in areas of high altitudes, as well as the air currents tend to be stronger, conditions that facilitate the occurrence and spread of fire (Cyr et al., 2007), (ii) with less tree canopy cover, such as grasslands and shrublands, whose biomass conditions are more flammable (Hoffmann et al., 2012), (iii) with a smaller water surface, as water courses can act as barriers to fire spread (Hellberg et al., 2004), (iv) closer to urban areas, given that human activities can be sources of ignition (Bowman et al., 2011).

2. Material and methods

2.1. Study area

The CDNP is a 152,400 ha Brazilian protected area located in the center of the state of Bahia, between longitudes 41°35' W - 41°15' W and latitudes 2°20' S - 12°25' S (Fig 1). The park, established in 1985, exhibits a mountain scenery with a mosaic of vegetation formations, including grasslands (“Campo Limpo”, “Campo Sujo” and Campo Rupestre”), savannas (“Cerrado stricto sensu”) and forests (“Matas or Floresta Estacional”) (ICMBio, 2007). In addition, the CDNP encompasses one of the highest portions of the Caatinga biome (i.e., the semiarid ecosystem of eastern South America), with altitudes ranging from 200 to 2000 m (Juncá et al., 2005). The climate of CDNP is classified as tropical semi-humid, with annual averages of temperature and precipitation of 24°C and 750 mm/year, respectively. The highest rainfall values are recorded from October to April (monthly mean rainfall = 160 mm) and the dry season comprises the months of May to September (monthly mean rainfall = 70 mm) (ICMBio, 2007).

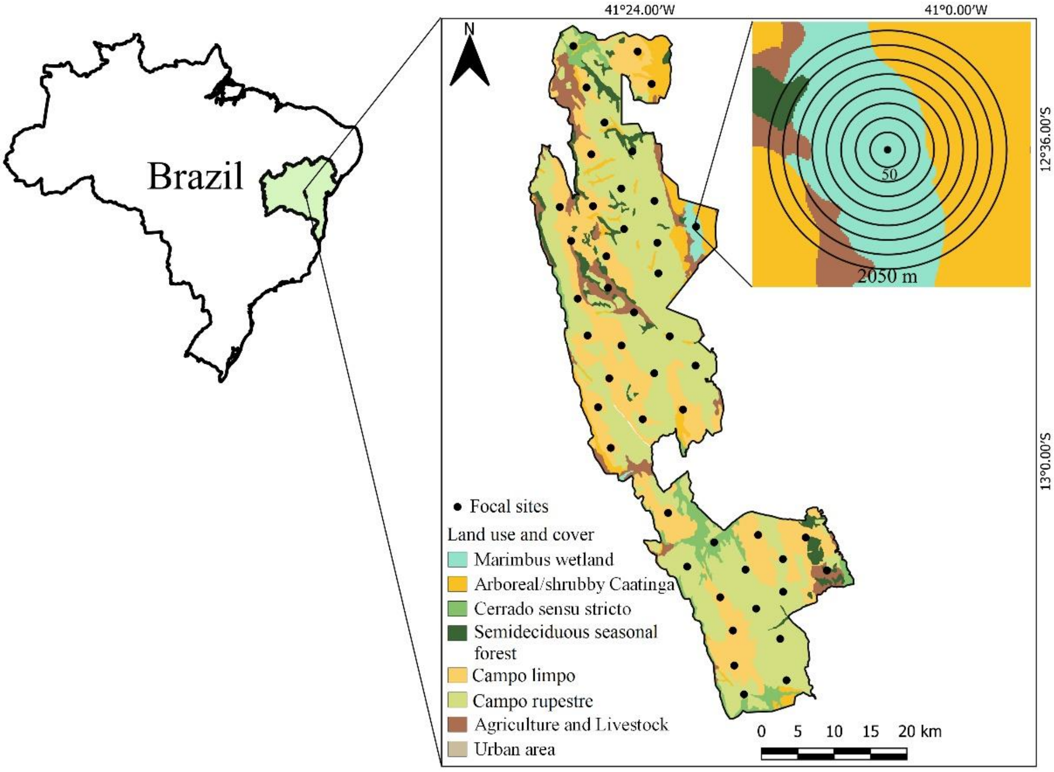

Fig. 1. Distribution of the 46 focal sites sampled in the Chapada Diamantina National Park (CDNP), Bahia, Brazil. Multiple buffers sizes (from 50 to 2050 m) are exhibited in the upper inset. Land use and cover were extracted from the vector map (PROBIO-Chapada Diamantina, Juncá et al., 2005). Available at: http://mapas.mma.gov.br/i3geo/datadownload.htm.

The CDNP has great relevance in the national context of conservation priorities, as it covers three Brazilian biomes (Caatinga, Cerrado and Atlantic Forest) and presents peculiar environments in the transition areas between these biomes, which harbor a great biological diversity (ICMBio, 2007). In addition, the scenic beauty existing in the park characterizes it as one of the main tourist centers in

Brazil. In fact, tourism is one of the main economic activities of several municipalities that surround the park, especially Andaraí, Ibicoara, Itaetê, Lençóis, Mucugê and Palmeiras (ICMBio, 2007), which together harbor about 75,500 people (IBGE, 2021). Despite a great part of local inhabitants recognizing the importance of the CDNP for the maintenance of natural resources and biodiversity in the region, many local communities perform several activities which are currently considered to be the main sources of ignition in the park (ICMBio, 2007). Fire is commonly used in the region for enhancing pasture growth to breed farm animals, plant extraction and mining, and can spread to greater extensions than planned due to the high flammability of the park's vegetation. Although there is an agreement that fire is a natural disturbance necessary for vegetation dynamic of the Cerrado (Durigan 2020; Schmidt and Eloy 2020), with several local initiatives to control and prevent fire, this is still considered the main environmental threat faced by the managers of the CDNP (Gonçalves et al., 2011).

2.2. Characterization of fire frequency and time since the last fire

We reconstruct the fire history from 1990 to 2019 across the CDNP by using the available Landsat 5, 7 and 8 (TM - Thematic Mapper; ETM+ - Enhanced Thematic Mapper Plus; and OLI - Operational Land Imager, respectively) satellite images (30 m of pixel size, 16 – days of temporal resolution). First, we used the Google Earth Engine platform to create Landsat mosaics for each year from 1990 to 2019. All available scenes for each year were used (an average of 19 scenes per year). In total, we used 225 scenes from Landsat 5 (from 1990 to 2011), 235 from Landsat 7 (from 1999 to 2019) and 132 from Landsat 8 (from 2013 to 2019). In this way, we created 30 Landsat mosaics, one for each year of the historical series (for more details, see Alencar et al., 2022). Then, still using the Google Earth Engine platform, we used two spectral indices to identify the burned areas – the maximum Normalized Burned Index (NBR) (Key and Benson, 2006) and the maximum Normalized Difference Vegetation Index (NDVI) (Rouse et al.,1974; Tucker 1979). These indices are widely used in several regions to assist in the identification of burned areas (Bastarrika et al., 2014; Alencar et al., 2022). The maximum NBR was used to identify burned areas for each year, creating an annual postfire image, while the maximum NDVI represented the best status that vegetation could achieve in a single growing season and was used as a proxy for vegetation state before fire, generating thus an annual non-burned area image (Bastarrika et al., 2014). We subsequently performed the visual detection and manual delineation of each fire scar based in the comparison between the annual maximum NBR and the annual maximum NDVI indices, adapting the method proposed by Alvarado et al., (2017). A total of 30 annual vector maps were produced, each one containing all fire scars that occurred within the CDNP at each year of the time series. All vector processing was performed on QGIS software v. 3.16 (QGIS Development Team, 2021),

Based on the reconstruction of the fire history, we estimated two key parameters to describe fire regimes – the fire frequency and the time since the last fire. The fire frequency refers to the number of times each pixel was burned during the study period (1990 to 2019). This parameter was estimated converting each annual vector map into a binary raster image (values of 1 for burned areas and 0 for unburned areas) with a spatial resolution of 30 meters to maintain the original resolution of the Landsat images. Then we summed the values of the overlapped layers of all annual raster images (30 images) by using the map algebra. We thus obtained a single raster image, in which each pixel value represents the fire count as proxy of the fire frequency. We also identified the year of the last fire per pixel, by reclassifying all pixel values = 1 by the number of the years from each annually burned area raster and then, to calculate with map algebra the maximum value of pixel of the overlapped layers of all 30 raster images. Finally, we identified the number of years elapsed since the last fire from 2019. All fire parameters were generated using the *rasterize* and *reclassify* function of the *raster* package (Hijmans, 2021) in the R software (R Core Team, 2021).

2.3. Landscape design and environmental factors

Finding the appropriate spatial scale to examine a given ecological process is essential for making correct interpretations of the research results (Jackson and Fahrig 2015). To establish which landscape scale would be adequate for each fire descriptor, we first identified the extent of each individual fire scar along the entire time series examined here (see Appendix S1, supplementary material). We detected that the smallest, greatest and mean extension of fire scars recorded was 44 m, 950 m and 255 m buffer radius (SD ± 588.47), respectively. Thus, we considered landscapes ranging from 50 m (lesser extent of fire scar) to 2050 m radius (equivalent to approximately twice the longest fire scar), with interval between buffer size of 250 m (equivalent to the mean extent of fire scars). After having established the scales of the landscapes (i.e., 2050 m) and subsequently the minimum distance to avoid overlapping them (i.e., 4100 m), we were able to select 46 focal sites aiming to cover the widest possible range of fire frequency across the CDNP (Fig. 1). We adopted a hybrid site-landscape approach, in which each response variable (fire frequency and time since the last fire) was evaluated within each focal site and predictors were measured at the landscape-scale within a specific radius (50 to 2050 m) from the center of each focal site (Tischendorf and Fahrig 2000). Both response variables were obtained considering a plot of 120 x 120 m around each focal site, which was based on the smallest size fire scar recorded along the study time period.

We extracted two environmental predictors at the patch-scale (i.e., focal sites) and three environmental predictors at the landscape-scale (Table 1). These five environmental predictors were estimated based on the pyrogeographic literature, which investigated the main modeling agents of fire regimes (Parisien and Moritz 2009; Vannière et al., 2008). In particular, three factors are related to natural conditions and resources and were measured at the landscape-scale: (i) tree canopy cover (in percentage) (data for 2015 derived from the Global Forest Cover Change (GFCC) Tree Cover Multi-Year Global 30 m, Sexton et al., 2013); (ii) mean altitude (in meters) (from TOPODATA online database, INPE, 2021); (iii) mean Normalized Difference Water Index (NDWI, McFeeters, 1996) (-1 to 1) (calculated using the Green and NIR bands of Landsat 8 – OLI images for the 26/10/2019, which detects the presence of water in the landscapes (Brubascher and Guasselli, 2013). We selected the month of October because it was a period with low clouds density images and enough water amount to distinct rivers and lakes, often dry during the dry season. It is important to notice that for the NDWI we used the green and near-infrared spectral bands for the index calculation, unlike the Normalized Difference Water Index- NDWI proposed by Gao (1996), who uses in the equation the two bands in the spectral band of the near-infrared (0.86 μm and 1.24 μm). Indeed, we choose the GFCC tree cover dataset from Sexton et al., (2013) because it was the most recent satellite product available with a 30 m spatial resolution, which could give more accurate measurements of tree cover compared to the MODIS products (500 m of spatial resolution) and is also the closest date available from the end of the fire history reconstruction.

At the patch-scale, we extracted (iv) the predominant land use and cover (rasterized from the vector map of CDNP land use and cover from Juncá et al., 2005), which is the most refined classification of land use and cover available for the study area and (v) the distance from each focal site to the nearest municipality, a proxy of human footprint (Table 1). Both response variables (fire frequency and time since the last fire), as well as environmental predictors were extracted using the *LecoS* complement v. 3.0 (Jung, 2016) and *calculate cover* function (Dodonov 2021) in QGIS (QGIS Development Team, 2021) and R software (R Core Team, 2021), respectively.

Table 1

Description of each environmental predictor evaluated in this study.

Environmental predictor	Description	Types	Range (mean ± SD)/ Effect scale		Data source
			Fire frequency	**Time since last fire**	
Predominant land use and cover	Land use and cover class present in at least 75% of each focal site	Patch	-	-	Vector map of CDNP land use and cover (Juncá et al., 2005)
Human footprint	Distance from each focal site to the nearest municipality (km)	Patch	9.27 − 28.62 (18.87 ± 4.81)	9.27 − 28.62 (18.87 ± 4.81)	This study
Tree canopy cover	Tree canopy coverage (%)	Landscape	18.35 − 57.35 (28.48 ± 7.63)/1050	19.67 − 54.77 (29.02 ± 7.66)/2050	This study
Mean elevation	Sum of the elevation values (m) of each pixel divided by the total number of landscape pixels	Landscape	335.82 − 1337.88 (1056.18 ± 248.29)/1550	333.56 − 1334.15 (1056.96 ± 249.33)/300	Digital Elevation Model (Topodata) (Valeriano et al., 2009)
Mean water surface	Sum of the NDWI (Normalized Difference Water Index) values of each pixel divided by the total number of pixels in the landscape	Landscape	-0.578 − -0.193 (-0.4 ± 0.07)/50	-0.56 − -0.35 (-0.42 ± 0.04)/2050	This study

2.4. Statistical analysis

We identified the appropriate spatial landscape size for further analysis (the so-called 'scale of effect', see Jackson and Fahrig 2012) of each landscape environmental predictor on both response variables through the *multifit* function (Huais, 2018), which uses the Criterion of Akaike Information (AIC) to measure the strength of the statistical models of each spatial scale evaluated (Appendix S3, supplementary material). Then, we evaluated the spatial correlation between all environmental predictors of each 46 focal sites using the Moran Autocorrelation Index (Gittleman and Kot 1990), with the *Moran.I* function of the *ape* package (Paradis and Schliep 2019). We thus used Generalized Additive Models for Location, Scale and Shape (GAMLSS) through the *gamlss* function of the *gamlss* package (Rigby and Stasinopoulos 2005) to assess the influence of environmental predictors on fire frequency and time since the last fire. This model class was chosen given that our response variable followed a distribution which cannot be fitted using more common model classes (e.g. Generalized Linear Models and Generalized Additive Models). Both of our response variables exhibited many zero values, which is related to the fact that several park locations had not been affected by fires during our study period. In particular, we used *Exponential Normal t* distribution and *Negative Binomial type I* distribution for fire frequency and time since the last fire, respectively. We created models containing all possible combinations of predictor variables, from the null to full model, in addition to the interacting model between tree canopy cover and mean altitude (total of 30 models, see appendix S3), using the *stepGAIC.VR* function in the *gamlss* package. Subsequently, the models were ranked based on the lowest Akaike information criteria corrected for small sample sizes (AICc). Therefore, models with ΔAICc values ≤ 2 and with scaled AICc values close to 1 were selected as best models explaining the variation in the data (Burnham and Anderson, 2002). It is worth mentioning that the scaled Akaike values (scaled AICc) produced for a set of GLMLSS have a similar concept to the AIC weights (wAIC) for a set of GLM. The scaled Akaike values produce a scaled classification of the models, given the relative importance of each one to explain the response variable (Rigby and Stasinopoulos 2005). All analyses were conducted in R software (R Core Team, 2021).

3. Results

We identified a large interannual variation in the total annual area burned in the CDNP from 1990 to 2019 (mean [±SD] = 68.55 km^2 [±103.96]). Specifically, 2008 was the year with the largest burned area (439 km^2) in the CDNP, while only 2.05 km^2 was burned in 1997 (Fig. 2).

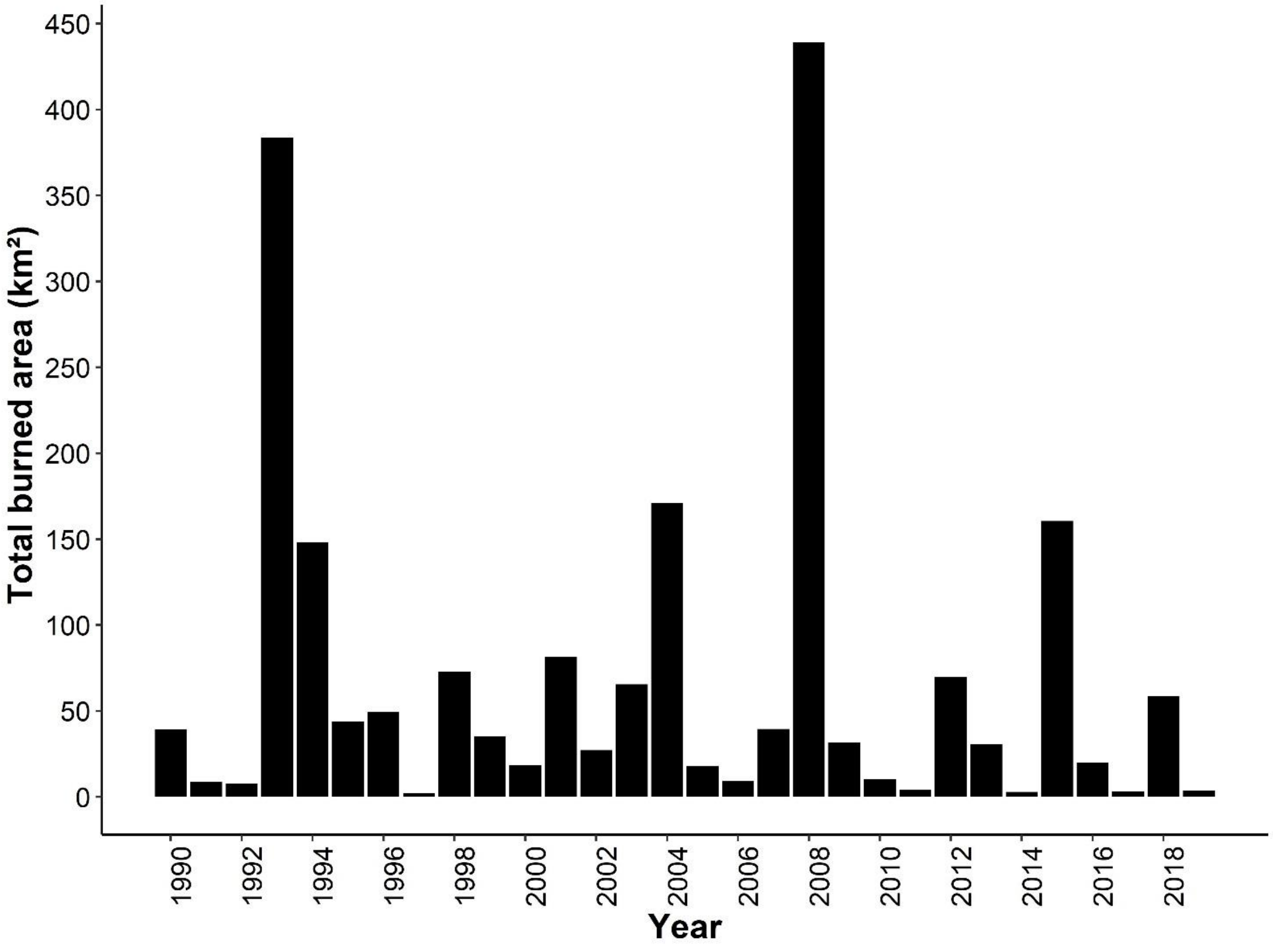

Fig. 2. Variation in the total annual area burned in the Chapada Diamantina National Park from 1990 to 2019.

We detected that 68% (1,030 km^2) of the park was burned at least once during the evaluated period, with the western region of the park exhibiting the highest fire frequency (Fig. 3a). Additionally, we observed that 50% of the total area burned at least twice between 1990 to 2019, 17% of the area was burned between three to five times and less than 1% burned more than five times along this period (Fig. 3b). Our findings also showed that about 32% of the park (486 km²) was not burned between 1990 and 2019 (Fig. 3b). We found that most of the eastern region of the park correspond to areas affected by older fires (1990-2000).

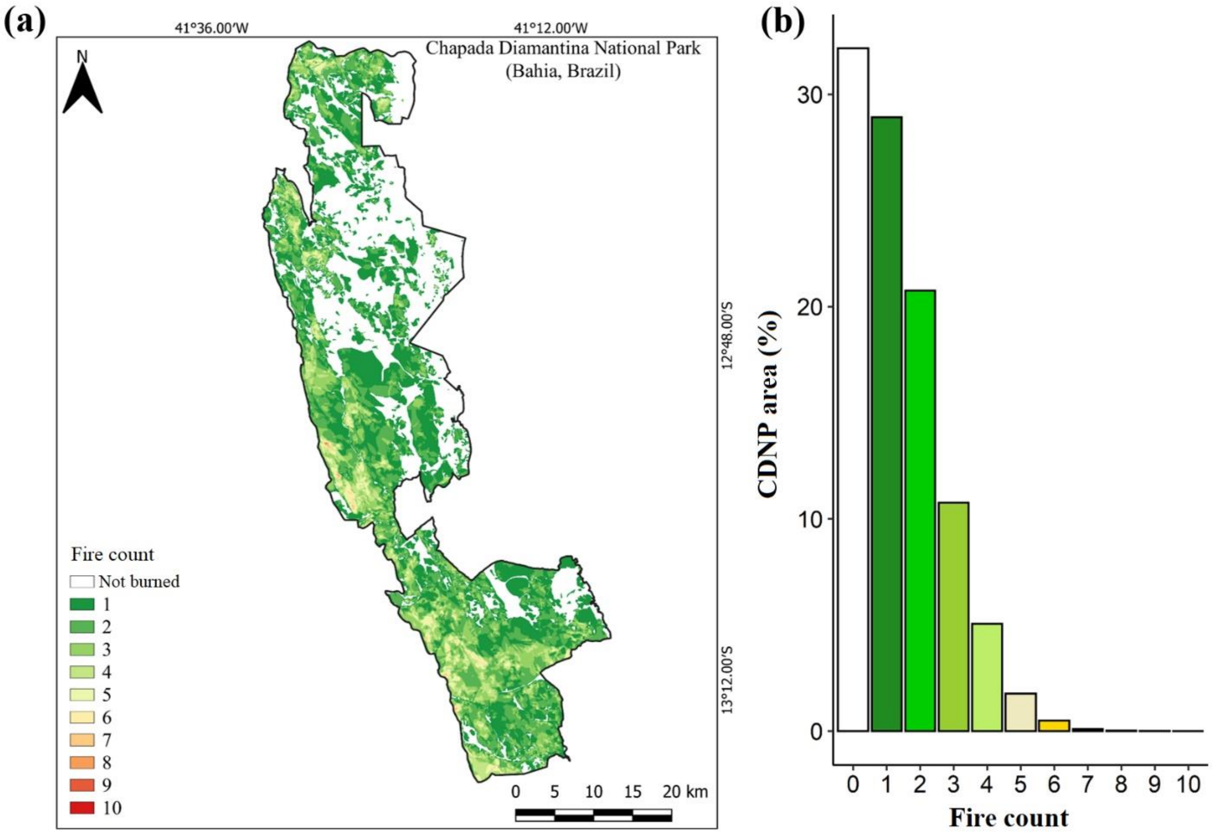

Fig. 3. (a) Map showing the fire frequency (fire count) from 1990 to 2019 in the Chapada Diamantina National Park; (b) Percentage of CNFAITH’S PHYLOGENETIC DIVERSITY area in each category of fire frequency.

Conversely, the western region was recently burned (Fig. 4a). We identified that out of the total of burned area (1,030 km²), 700 km² (68%) was burned during the last 15 years (from 2005 to 2019) while 330 km² (32%) burned between 1990 to 2004 (Fig. 4b).

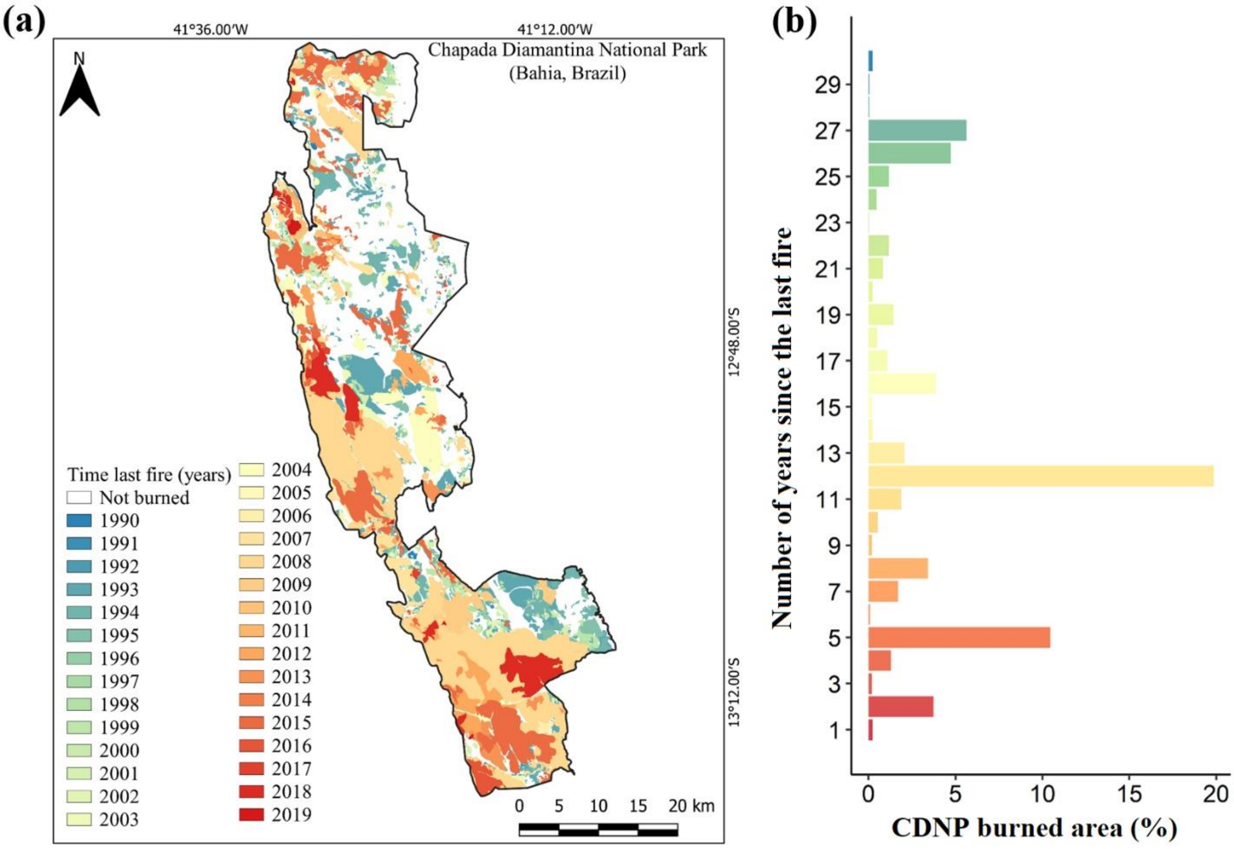

Fig. 4. (a) Map showing the time since the last fire from 1990 to 2019 across the Chapada Diamantina National Park; (b) percentage of the area burned at each year, in relation to the total area of the park.

Based on GAMLSS and model selection procedure, we detected that only one model was parsimonious (ΔAICc ≤ 2) in explaining patterns of fire frequency in the CDNP (Table 2). In particular, the predominant land use type and the distance between the nearest municipality were negatively related to the mean fire frequency (Fig. 5a, b). Conversely, we observed a positive effect of the water surface on the mean fire frequency in the park (Fig. 5c). In addition, we found three parsimonious models to explain the time since the last fire (Table 2). In summary, they demonstrate that mean altitude and tree canopy cover have a slight positive effect on this fire parameter (Fig. 5d, e), indicating that the most recent fires in the park occurred in lower landscapes and with less tree cover.

Table 2

Set of candidate models developed (ascending order of AICc) to explain the fire frequency and time since the last fire in the Chapada Diamantina National Park, Bahia, Brazil. d.f. = degrees of freedom; AICc = Akaike Information Criteria; ΔAICc = difference between a given model and the best model; Scaled AICc = relative importance of models, ranging from 0-1.

Response variable/Model	**d.f**	**AICc**	**ΔAICc**	**Scaled AICc**
Mean fire frequency				
1: Predominant land use and cover + Distance to the nearest municipality + Water surface	9	189.83	0.00	1.00
2: Distance to the nearest municipality + Water surface	4	193.90	4.07	0.86
3: Distance to the nearest municipality + Water surface + Tree canopy cover	5	194.53	4.70	0.84
4: Distance to the nearest municipality + Water surface + Tree canopy cover + Mean altitude	6	196.23	6.40	0.79
5: Predominant land use and cover + Distance to the nearest municipality + Water surface + Tree canopy cover	10	197.24	7.41	0.75
6: Predominant land use and cover + Water surface	8	197.74	7.91	0.74
7: Predominant land use and cover + Water surface + Tree canopy cover	9	198.93	9.10	0.70
8: Predominant land use and cover + Distance to the nearest municipality + Water surface + Mean altitude	10	200.97	11.14	0.63
9: Predominant land use and cover + Distance to the nearest municipality + Water surface + Mean altitude +Tree canopy cover	11	204.63	14.80	0.51
10: Predominant land use and cover + Distance to the nearest municipality + Mean altitude +Tree canopy cover	10	209.69	19.86	0.35
11: Predominant land use and cover + Water surface + Mean altitude + Tree canopy cover	10	209.89	20.05	0.34
12: Predominant land use and cover + Distance to the nearest municipality +Tree canopy cover	9	212.96	23.13	0.24
13: Predominant land use and cover + Distance to the nearest municipality	8	213.85	24.02	0.21
14: Model null (contains only the intercept)	2	219.69	14.80	0.51
15: Interaction between mean altitude and tree canopy cover	3	220.39	30.56	0.00
Time since last fire				
1: Mean altitude + Tree canopy cover	4	293.77	0.00	1.00
2: Tree canopy cover	3	294.05	0.28	0.97
3: Interaction between mean altitude and tree canopy cover	3	294.19	0.42	0.96
4: Model null (contains only the intercept)	2	294.73	0.96	0.92

5: Water surface + Tree canopy cover	4	294.88	1.11	0.90
6: Water surface + Mean altitude + Tree canopy cover	5	295.40	1.63	0.86
7: Distance to the nearest municipality + Mean altitude + Tree canopy cover	5	295.46	1.69	0.86
8: Distance to the nearest municipality + Water surface + Mean altitude + Tree canopy cover	6	296.25	2.48	0.79
9: Distance to the nearest municipality + Water surface + Tree canopy cover	5	296.54	2.77	0.77
10: Water surface + Mean altitude	4	298.04	4.27	0.65
11: Predominant land use and cover + Mean altitude + Tree canopy cover	9	300.45	6.68	0.45
12: Distance to the nearest municipality + Water surface + Mean altitude	9	300.56	6.79	0.44
13: Predominant land use and cover + Distance to the nearest municipality + Mean altitude + Tree canopy cover	10	303.06	9.29	0.24
14: Predominant land use and cover + Distance to the nearest municipality + Water surface + Tree canopy cover	10	303.33	9.56	0.22
15: Predominant land use and cover + Water surface + Mean altitude + Tree canopy cover	10	303.59	9.82	0.19

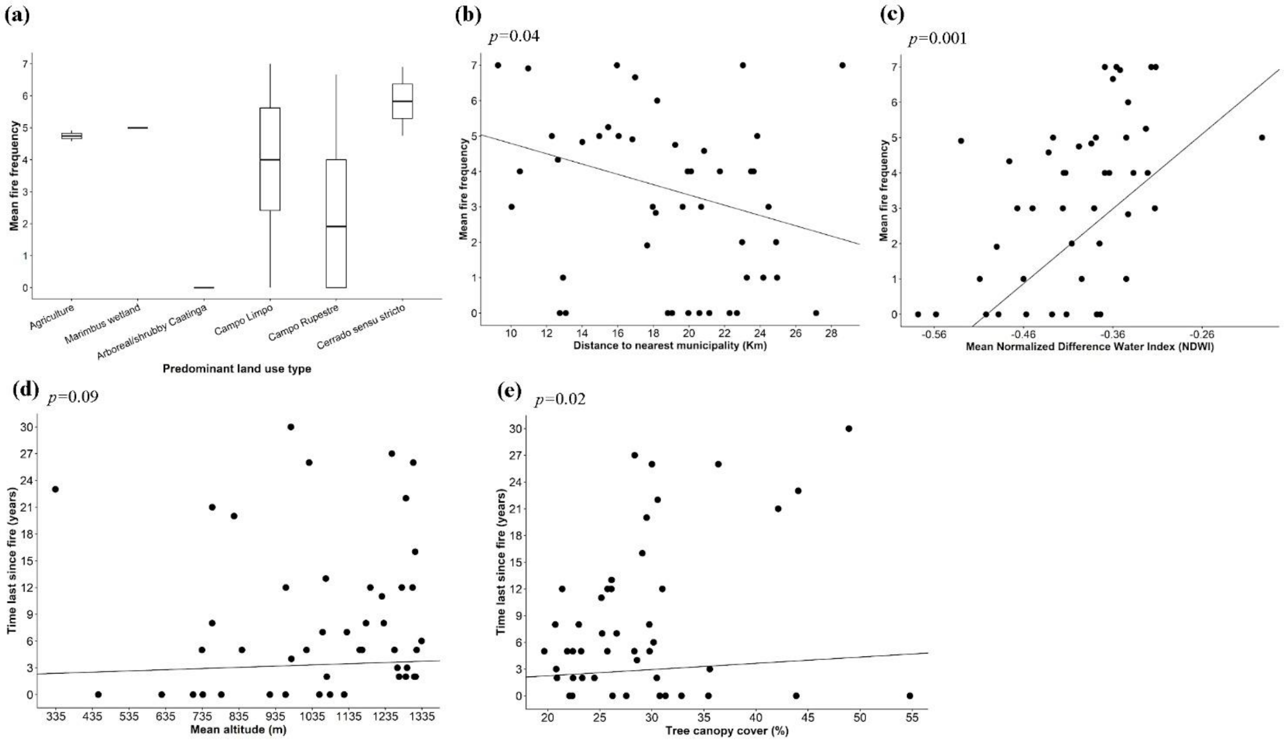

Fig. 5. Relationships between the environmental predictors included in the most parsimonious model used to explain the mean fire frequency and the time since last fire in the Chapada Diamantina National Park. Relationship between mean fire frequency and (a) Predominant land use and cover;

(b) Distance to the nearest municipality; (c) Mean Normalized Difference Water Index. Relationship between time since last fire and (d) Mean altitude; (e) Tree canopy cover.

4. Discussion

We provide the first assessment on how environmental factors acting in distinct spatial scales shape two properties of the fire regime in a Brazilian savanna ecosystem. The mean fire frequency and time since the last fire were highly variable across the entire CDNP, reflecting the strong influence of landscape heterogeneity on fire regime. Specifically, we have shown that the predominant land use type and the distance to the nearest municipality were negatively related to the fire frequency, while water surface had a positive effect on this parameter. Furthermore, we found that only tree canopy cover and altitude were selected as good predictors of the time since the last fire. Along the period herein evaluated, the CDNP was characterized by a large interannual variation of the total burned area, which is in turn mainly determined by conditions (humidity) and amount of fuel (biomass) available for burning (Archibald et al., 2009).

We observed that large areas of the park had burned in 1993 and 1994, period that coincides with the El Niño phenomenon of moderate intensity (INPE, 2021), and which likely influenced the fire occurrence in these years (Mesquita et al., 2011). Although 2010 was one of the years with the highest record of burned area in Brazilian flammable ecosystems in the last 20 years (Pereira et al., 2021), we recorded one of the smallest annual burned area for the CDNP.

We revealed a clear heterogeneous fire occurrence across the CDNP, in which extensive areas were unburned (32%), some restricted areas had high fire occurrence, but most areas showed low to moderate fire frequencies within their landscapes. Compared to other flammable ecosystems and protected areas in Brazil, the CDNP presents a higher unburned area (Alvarado et al., 2018; Pereira Júnior et al., 2014; Silva et al., 2020). In general, we identified that areas with lower fire frequency are restricted to the central-north and eastern portion of the park. These regions are formed by a set of parallel mountain ranges and deep valleys covered by forest formations (Mesquita et al., 2011). In addition to the difficult human accessibility in these regions, the high humidity contained in the dense forest vegetation potentially represents a barrier to both ignition and propagation of fires.

Another factor to be considered is that the eastern region outside the park's boundaries is characterized by a greater abundance of seasonal semideciduous forest fragments, while the western portion outside the park is marked by the predominance of agricultural areas (ICMBio, 2007). Although this was not herein assessed, we strongly suggest that future studies incorporate the influence of land use and cover surrounding protected areas, given the potential role of certain anthropogenic activities in affecting fire regime (see Conciani et al., 2021). Conversely, the western region of the park was most frequently burned, which might be related to the higher anthropogenic activities in this region combined to the high human density in the park’s surrounding. The southwestern region of the CDNP exhibited high fire frequency, likely related to evergreen plants (*Helichrysum bracteatum*) collectors, who usually set fire to the areas where this species occurs to enhance flowering in the next season (ICMBio, 2007).

We detected that the predominant land use type explained park's fire frequency patterns. In particular, both “Marimbus wetland” and “Cerrado sensu stricto”, which we previously expected to present a low fire frequency due to the higher humidity generally retained in these vegetations, were the land cover exhibiting the highest fire frequency. The Marimbus wetland formations are located in a peculiar region of the park where extensive areas are periodically flooded, which favors fuel build-up. In a scenario of intense and prolonged drought, this large amount of biomass can lose a lot of moisture and become highly flammable, contributing to the highest fire frequency in this region.

Furthermore, we expected that the focal sites with local predominance of “Campo Limpo” and “Campo Rupestre” would have a higher fire occurrence, given that they contain fuels that are more prone to ignition and therefore are considered highly flammable (Hoffmann et al., 2012). However, contrary to our expectations, we found that these environments may also be less affected by fire. This can be understood by the fact that the "Campo Rupestre" is formed by vegetation with a low growth rate, a sparse distribution of herbaceous growth and a higher percentage of bare soil and rocks, which defines its lower fire occurrence (Alvarado et al., 2017). Such characteristics promote fuel discontinuity, significantly reducing the fire propagation in landscapes dominated by this vegetation (Cyr et al., 2007).

Water courses, such as lakes, rivers and streams, although recognized to act as natural firebreaks avoiding fire propagation in the landscape (Hellberg et al., 2004), were positively related to higher fire frequencies in the studied protected area. Although this result may initially seem contradictory, it could be associated to the greater flow of tourists in landscapes exhibiting high abundance of water attractions, such as waterfalls. The disorderly visitation has been identified as one of the main factors responsible for fire occurrence in the park's environments (ICMBio, 2007), and, therefore, may be related to the higher fire frequency observed in landscapes with greater average of water surface.

We also identified that the mean altitude and tree canopy cover at the landscape scale influenced the time since the last fire. In general, the oldest fires in the park occurred in higher areas compared to more recent fires. Most recent fires in the CDNP are probably human-made, while the oldest fires are probably of natural origin (ICMBIO, 2007). In fact, natural fires tend to occur in higher landscapes, given the higher probability of lightning strikes in these areas (Cyr et al., 2007). The most recent fire occurrence in lower altitudes can be understood by the ease of human access to these environments, which is currently considered the main source of fire ignition in the park. We further noted that the most recent fires mostly occurred in landscapes exhibiting low tree canopy cover, indicating that both grassland and savanna vegetation of the CDNP is currently more affected by fire than the forest formations. In fact, tree cover > 40% can limit fire incidence and spread on savanna vegetation (Archibald et al., 2009).

Finally, we highlight that 68% of the total area burned in the CDNP between 1990 and 2019 was affected by fire in the 15 most recent years of the evaluated series, coinciding with the period in which the fire management actions were already carried out (Gonçalves et al., 2011). Fire use practices carried out by traditional people within the CDNP are heavily criminalized and fought by law (ICMBio, 2007; Gonçalves et al., 2011). The fire exclusion policies adopted by the CDNP since 2001, added to the anthropogenic activities in the park have contributed to the homogenization of fuel load distribution across the park and thus increased the risks of large-scale fires (Fidelis et al 2018). Several studies have shown that maximum fire suppression can be a driver of intensifying fire regimes and is certainly an ineffective practice for tropical grassland and savanna ecosystems (Alvarado et al., 2018; Conciani et al., 2021; Durigan and Ratter 2016; Durigan 2020; Schmidt and Eloy 2020). This policy is on the wrong way for the good functioning of flammable ecosystems, in which periodic fires are important for the creation and maintenance of the structure, composition, function, evolution and ecological integrity of their landscapes (Pivello 2011; Simon et al., 2009).

In response to this scenario, since 2014 the Chico Mendes Institute for Biodiversity Conservation - ICMBio (the environmental agency of the Brazilian government) initiated a program entitled Integrated Fire Management (IFM) in protected areas (Schmidt et al., 2018). This program consists of introducing prescribed fires at the beginning of the dry season or other interventions of fire management by local communities and protected area managers. The main goal is to create landscape mosaics with different fire histories, promoting a fuel discontinuity in the landscapes and thus protecting the more sensitive vegetation from large and severe fires (Schmidt et al., 2018).

To summarize, the IFM program is based on hiring and training residents of local communities as fire management agents to carry out prescribed burn and fire management, thus incorporating the ecological knowledge of traditional people into the proper fire management in each region (Mistry et al., 2018; Schmidt et al., 2018). Despite being an innovative proposal and still under analysis in the Brazilian federal parliament (PL 11276/2018, 2021), the experimental implementation of the IFM in three Brazilian protected areas brought satisfactory results to reduce large and severe fires in these regions (Eloy et al., 2019; Schmidt et al., 2018). Given the CDNP socio-environmental context, we believe that the integration between fire use practices by traditional communities and scientific knowledge about fire ecology is a crucial approach to promote proper fire management in this protected area, thus reducing the frequency of severe fires and the costs involved in mitigating them and maintaining the livelihoods of communities in and around the park.

5. Conclusions

We witness a current Brazilian political scenario, whose environmental issues are mostly ignored, and severe budget cuts are applied under national environmental institutions, compromising actions for the conservation of biomes and biodiversity (Ferrante and Fearnside 2021). In view of this, it poses extremely necessary to use scientific knowledge to assist in future management decisions, in order to deliver the scarce resources towards priority conservation actions.

Here, we have shown that in the evaluated period there is a greater and more recent action of fire in the western region of the park. In addition, the highest fire frequencies are positively related to the existing water surface in the landscapes and negatively related to the proximity of urban settlements and therefore, we recommend that fire monitoring activities in the CDNP should be reinforced and prioritized in landscapes located in the western region of the park, within altitudes above 600 meters, presenting grasslands vegetation (e.g. "Campo limpo" and "Campo rupestre"), and containing higher abundance of aquatic formations (e.g. waterfalls), which generally attract a large number of tourists.

Since 2002, the official brigade of the Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA) has been working at the CDNP, with around 150 trained members (volunteers and contractors) who play a fundamental role in preventing and fighting fires throughout the park. However, we demonstrate that the most recent fires (from 2005 to 2019) have reached larger areas of the park compared to older fires, which indicates that maximum fire suppression adopted to date, may not be the most appropriate fire management for existing ecosystems at CDPN. Instead, as discussed earlier, integrated fire management would configure a management strategy more suited to both park conservation and local communities.

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SUPLEMENTARY MATERIAL

Patch and landscape features drive fire regime in a Brazilian flammable ecosystem

Amanda G. Anjos[1], Swanni T. Alvarado[2,3], Mirco Solé[4,5] & Maíra Benchimol[4]

[1]*Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, CEP 45662-900, Ilhéus, Bahia, Brazil*

[2]*Programa de Pós-graduação em Agricultura e Ambiente, Universidade Estadual do Maranhão, Praça Gonçalves Dias, CEP 65800-000, Balsas, Maranhão, Brazil*

[3]*Programa de Pós-graduação em Geografia, Natureza e Dinâmica do Espaço, Universidade Estadual do Maranhão, Avenida Lourenço Vieira da Silva, Jardim São Cristóvão, CEP 65055-310, São Luís, Maranhão, Brazil*

[4]*Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, 45662-900, Ilhéus, Bahia, Brazil*

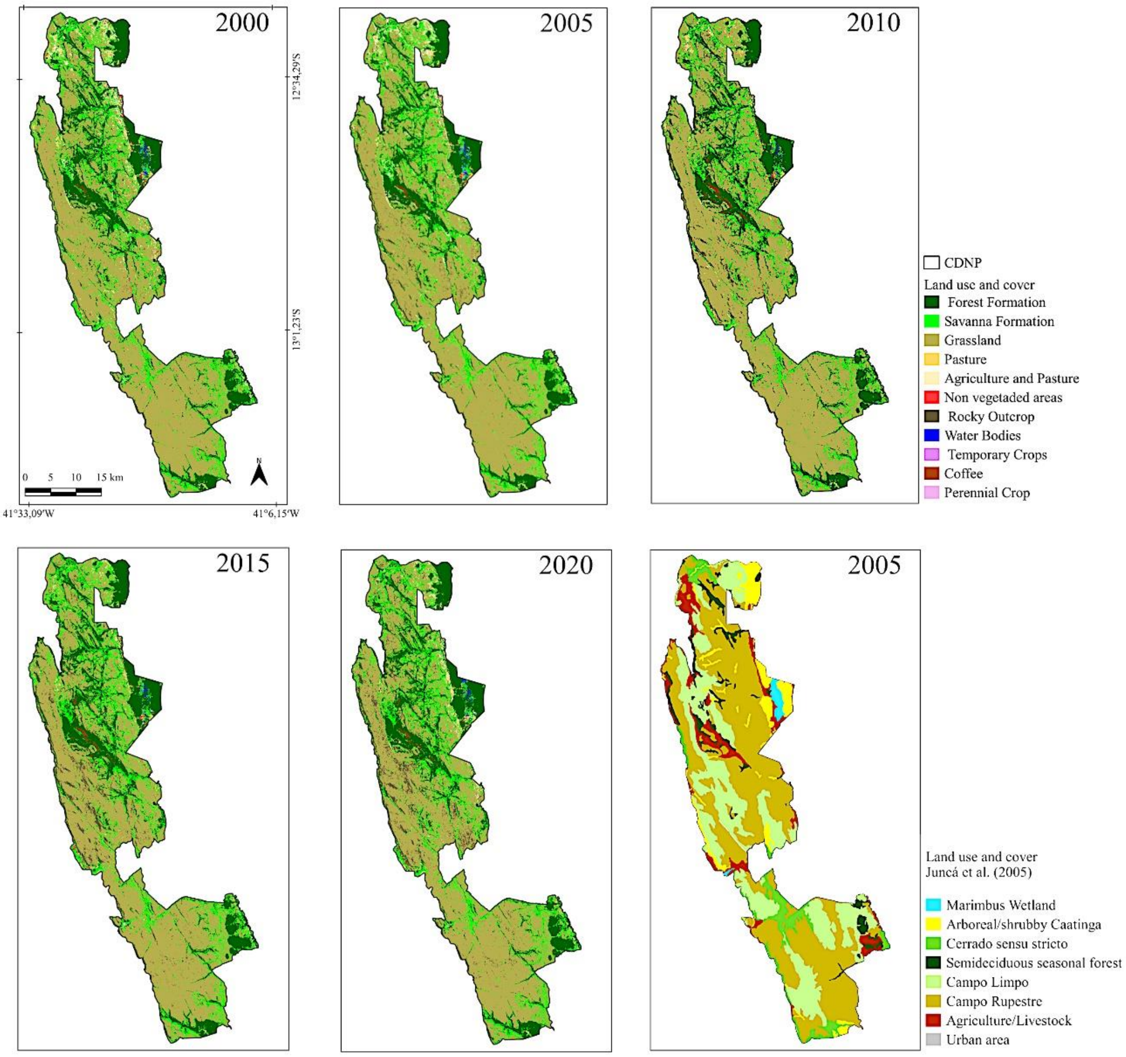
[5]*Herpetology Section, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany*

Corresponding author: Amanda G. dos Anjos, Email: amandaanjos09@gmail.com

Appendix S1. Method for calculating the extent of fire scars in Chapada Diamantina National Park, Bahia, Brazil.

We first identified the centroid of each fire scar polygon to obtain the extent of fire scars that occurred in the CDNP from 1990 to 2019. Then, we measured the distance (in meters) from the centroid to perimeter of the polygon. Given that irregular shape of the fire scars polygons, we performed 20 distance measurements, and calculated the average distance from the centroid to the perimeter of each polygon. This distance was used as a proxy for the average extension of each fire scar. Distances were calculated using the *Distance to nearest hub* function in QGIS software (QGIS Development Team, 2021). The fire polygon with the smallest average distance from the centroid to its perimeter presented a value of 44.5 m (lesser extent of fire scar). The polygon with the greatest average distance was 963.8 m (longest fire scar). The average extent of fire scars in the entire time series was 245.3 m therefore, we used this value to determine the interval between the scales.

Appendix S2. Maps demonstrating the stability of land use and cover in Chapada Diamantina National Park over two decades. The first five maps are based on MapBiomas data (Collection 6, Souza et al., 2020). The last map (used in this study) is based on the more detailed classification provided by Juncá et al., 2005.



Appendix S3. Scale of effect of landscape environmental factors on fire frequency and time since last fire.

Of the five environmental predictors considered in the research, three (tree canopy cover, mean altitude and mean water surface) were calculated in nine different sized buffers (landscapes), ranging from 50 to 2050 m in radius, based on the method described in Appendix S1. Then, we evaluated the strength of the relationship between each environmental predictor and the response variables (fire frequency and time since the last fire) at each spatial scale using the Criterion of Akaike Information (AIC). The lowest value of this metric indicates the spatial extent of the landscape within which the response variables are most strongly related to the environmental predictors (Huais, 2018). Finally, environmental predictors were included in the statistical models (GAMLSS), each one in its identified effect scale.

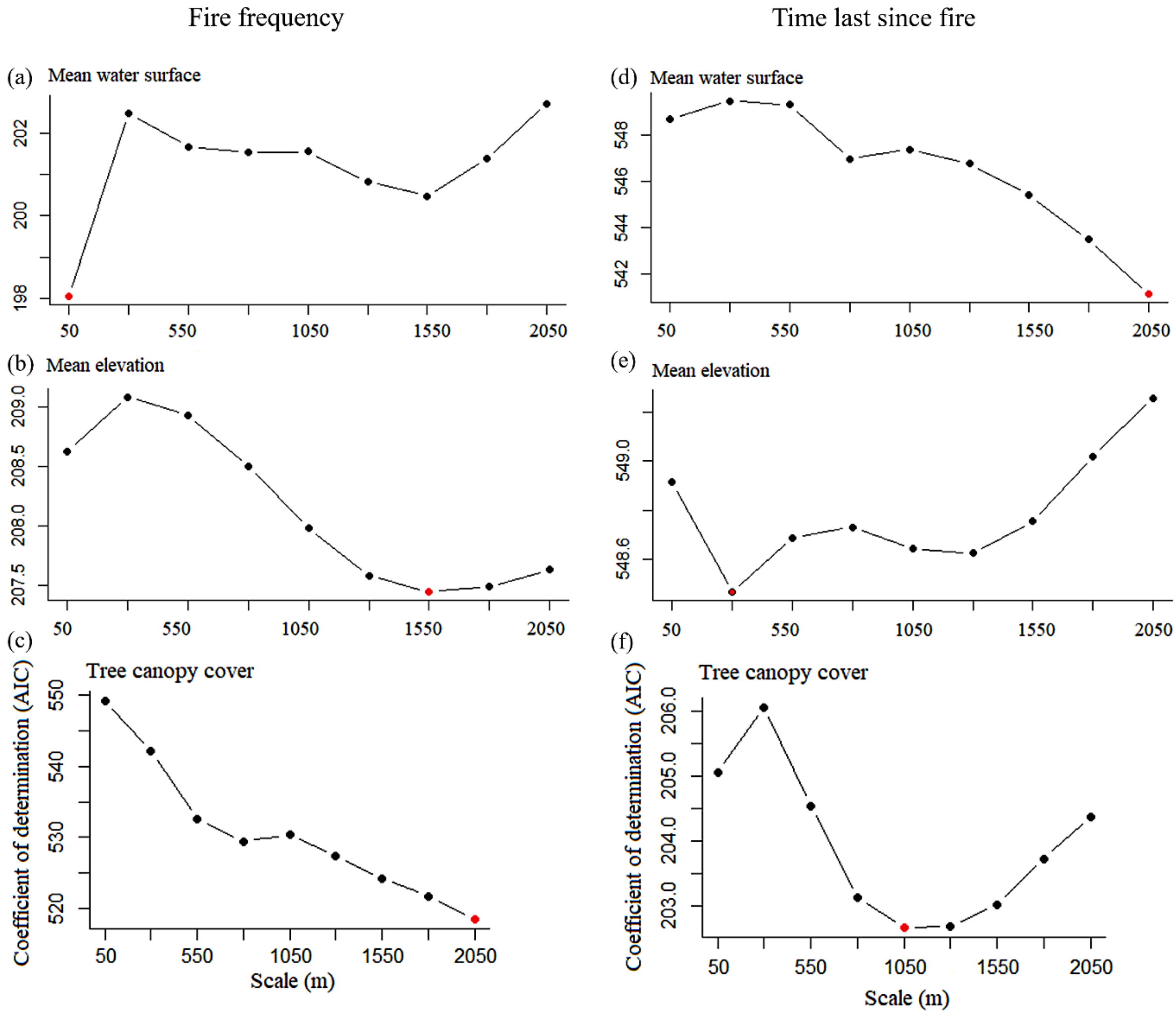


Fig.S1. Association between landscape size (x-axis) and the strength of the relationship (AIC=Akaike Information Criteria, y-axis) between each environmental predictor and the response variables (fire frequency and time since the last fire). The smallest AIC value represents the strongest relationship. The size of the landscape used in the statistical models is indicated by the red dot.

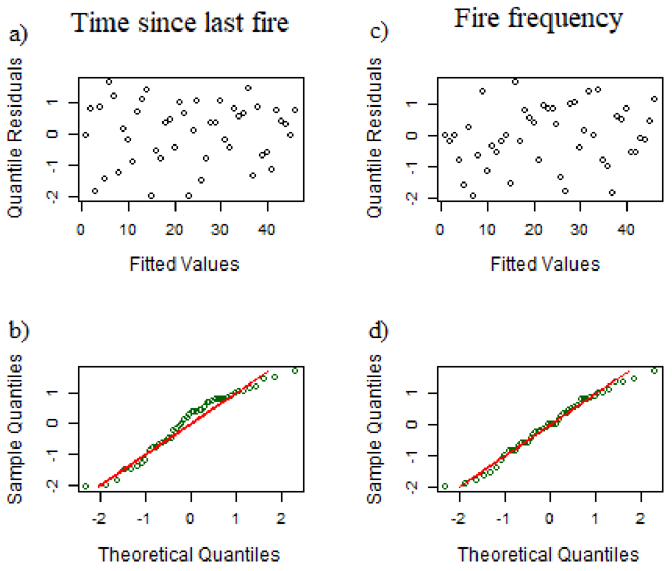


Fig.S2. Residual graphs for diagnostic the fit of the models that best explained the variation in the fire frequency and the time since the last fire (Table 2, models 1). a) and c) scatter plot of residuals against predicted values; b) and d) the QQ-normal plot of the residuals.

Appendix S5. Parameters and estimated p-values for each environmental predictor of the best models explaining the mean fire frequency and the time since the last fire in the Chapada Diamantina National Park

Model	**Estimate**	**p-value**
Mean fire frequency		
Model 1: Predominant land use - Marimbus wetland	-6.24	0.007
Predominant land use - Caatinga Arbórea/Arbustiva	-3.52	0.063
Predominant land use - Campo Limpo	-3.08	0.012
Predominant land use - Campo Rupestre	-3.19	0.006
Predominant land use - Cerrado	-1.70	0.266
Distance to the nearest municipality	-0.14	0.041
Water surface	21.16	<0.001
Time since last fire		
Model 1: Mean altitude	0.001	0.0985
Tree canopy cover	0.06	0.0263

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CAPÍTULO 3

Fire frequency and tree cover are determinants the taxonomic and phylogenetic diversity of anuran communities in a unique Brazilian flammable ecosystem

Manuscrito em preparação

Imagem de Costa, R.N.

Fire frequency and tree cover determine the taxonomic and phylogenetic diversity of anuran communities in a unique Brazilian flammable ecosystem

Amanda G. Anjos[1]*, Swanni T. Alvarado[2,3], Mirco Solé[4,5] and Maíra Benchimol[4]

[1]*Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, CEP 45662-900, Ilhéus, Bahia, Brazil*

[2] *Programa de Pós-graduação em Agricultura e Ambiente, Universidade Estadual do Maranhão, Praça Gonçalves Dias, CEP 65800-000, Balsas, Maranhão, Brazil*

[3]*Programa de Pós-graduação em Geografia, Natureza e Dinâmica do Espaço, Universidade Estadual do Maranhão, Avenida Lourenço Vieira da Silva, Jardim São Cristóvão, CEP 65055-310, São Luís, Maranhão, Brazil*

[4]*Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, 45662-900, Ilhéus, Bahia, Brazil*

[5]*Herpetology Section, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany*

Corresponding author: Amanda G. Anjos, Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, CEP 45662-900, Ilhéus, Bahia, Brazil. E-mail: amandaanjos09@gmail.com (Anjos, A. G.). Telephone: +55 32 99830-9768

ABSTRACT

Fire is a natural disturbance that has shaped Earth's biodiversity for millions of years. In flammable ecosystems, fire is an important environmental filter, selecting certain species exhibiting characteristics that make them tolerant of post-fire environmental conditions.

Here, we evaluated the effects of fire regime parameters, in addition to local environmental and landscape characteristics on the taxonomic and phylogenetic diversity of anuran communities within a protected area of Brazilian savanna. We found that fire frequency and the extend of the burned area were the most important predictors of anuran taxonomic and phylogenetic richness, whereas the divergence and phylogenetic structure were best explained by the tree canopy cover and the water body margin heterogeneity. Intermediate fire frequencies led to an increase in species richness and phylogenetic overdispersion of anuran communities. Finally, our results indicate that the environmental heterogeneity as measured by a greater tree cover and a greater margin heterogeneity allow the co-occurrence of species exhibiting different ecological requirements, thus promoting phylogenetic overdispersion. We reinforce the importance of including all facets of diversity to better understand how fire and local and landscape environmental features structure the diversity of frog communities. The maintenance of native forest cover can ensure higher diversity of anurans in flammable ecosystems.

Keywords: environmental filtering, anuran assemblage, phylogenetic structure, species richness

1. Introduction

Understanding how biotic and abiotic factors shape species distribution in space is one of the central questions of ecology (Chase, 2003). In fact, biological communities are not formed by a random association of species, but by species that, depending on the environmental conditions, may compete or share resources (Wiens, 2011). For instance, more complex environments tend to have a greater diversity of microhabitats, which allows for the differentiated use of resources and thus favoring the coexistence of species (Conte and Rossa-Feres 2007; Vasconcelos et al., 2009). The opposite is expected for more homogeneous environments and/or with more severe environmental conditions, in which species compete for limited resources potentially leading to the competitive exclusion of one or more species (Vamosi et al., 2009). Thus, the integration between environmental conditions and ecological interactions is fundamental to explain the structure of biological communities, and therefore provide knowledge to contribute for the maintenance and conservation of species in natural ecosystems (Gaston, 2000).

Integrated with environmental factors, ecological disturbances can lead to substantial changes in community composition (Chase, 2003). Fire is a natural disturbance that has shaped Earth's biodiversity for millions of years (Bowman et al., 2009). Although its incidence initially causes damage to organisms, natural fire regimes allow many plants to complete their life cycles (Rundel et al., 2018), create habitats for several animals (Kelly et al., 2017) and influence important ecosystem processes (Pausas and Keeley, 2019). Furthermore, in ecosystems evolutionarily dependent on fire (also known as flammable ecosystems), fire is as an important environmental filter, selecting groups of species with traits that allow tolerance and resistance to it (He et al., 2019).

Frog communities are strongly shaped by local habitat conditions (Duellman and Trueb, 1994) such as temperature, humidity, precipitation (Buckley and Jetz, 2007; Werner et al., 2007; Vasconcelos et al., 2010), presence and characteristics of water bodies (Santos et al., 2007; Navas and Otani, 2007; Provete et al., 2014) and vegetation inside and around the water body (Burne and Griffin, 2005, Keller et al., 2009; Vasconcelos et al., 2009). Given that frogs are ectothermic, exhibit highly permeable skin, limited dispersion capacity and complex life cycles, they are strongly affected by environmental changes (Katzenberger et al., 2012). Frogs are strongly affected by environmental changes because of their thermal physiology, have highly permeable skin, limited dispersal ability, and complex life cycles (Katzenberger et al., 2012). There has been a growing effort to assess how human activities have modified frog’s natural habitats, investigating environmental changes, both at a local and landscape scales (Prado and Rossa-Feres, 2014; Almeida-Gomes et al., 2016a; Ribeiro et al., 2016; Holtmann et al., 2017; Wright et al., 2020). However, most studies have focused primarily on assessing the effect of changes in land use and climatic conditions on frogs, and little is known about how fire affects anuran assemblages, especially in flammable ecosystems, such as tropical and temperate savannas (Anjos et al., 2021).

Phylogenetic diversity (PD) is the diversity facet that incorporates evolutionary relationships between species (Magurran, 2004). Unlike measures of taxonomic diversity, PD allows a more precise distinction of the ecological roles of each species in the community, since they are considered as entities that carry unique evolutionary histories (Pellens and Grandcolas, 2016). In addition, given that most species characteristics tend to be conserved across evolutionary lineages (Blomberg et al., 2013), PD can also represent the functional diversity of communities, which is often difficult to estimate for groups whose knowledge of their functional characteristics is quite limited (Cadotte et al., 2011; Winter et al., 2013). In addition to these factors, PD characterizes the evolutionary potential of lineages to respond to environmental changes (Cisneros et al., 2014) and, therefore, has progressively been recognized as an essential dimension of diversity for maintaining biodiversity (Pollock et al., 2017).

Here, we assess how both the taxonomic and phylogenetic diversity of anuran communities have responded to fire disturbance and a set of local and landscape features, across contrasting landscapes distributed in a flammable protected area of the Brazilian savannah. We hypothesized that fire regime properties (i.e. fire frequency, burned cover area and time since the last fire) in the last 30 years are the main drivers of frog taxonomic diversity, given the central role of fires in structuring biological communities in flammable ecosystems (He et al., 2019). In relation to phylogenetic diversity, we predicted that anuran communities in landscapes more severely affected by fires (i.e., higher fire frequencies, greater amount of burned area and more recent fires) will contain more closely-related species, given that this disturbance selects for species that can cope with environmental changes triggered by fire, thus promoting phylogenetic clustering (Verdú and Pausas, 2007). We expect to contribute to the understanding of the key drivers explaining diversity patterns of anurans in fire-disturbed ecosystems. Our results can also provide suggestions for fire management actions to preserve both species richness and evolutionary potential of anuran communities in this protected area.

2. Material and Methods

2.1. Study area

We conducted this study in the Chapada Diamantina National Park (CDPN), located in the center of the Brazilian state of Bahia, a region that corresponds to the northern portion of the Espinhaço mountain range (Fig. 1). The CDNP was created in 1985 and represents a unique Brazilian protected area, as it covers three Brazilian biomes (*Caatinga* and the global biodiversity hotspots *Cerrado* and *Atlantic Forest*), with a mosaic of vegetation types, ranging from grasslands to forests formations (Santos et al., 2020). The climate is classified as tropical semi-humid, with annual averages of temperature and precipitation of 24 °C and 750 mm/year, respectively (Teixeira et al., 2005).

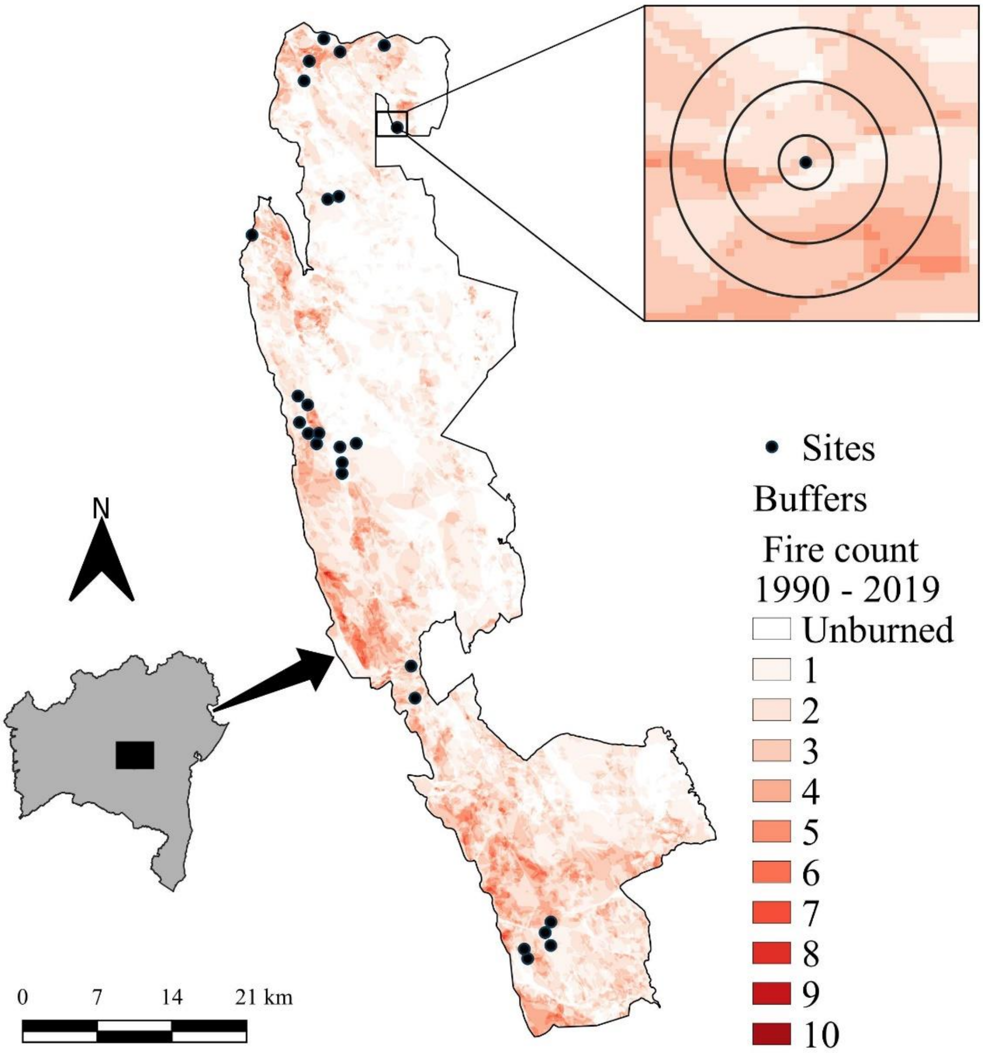

Figure 1. Location of the 26 sites sampled in the Chapada Diamantina National Park and number of times each area was burned in the last 30 years (fire count).

The park is a naturally fire-prone environment, mainly due to the high flammability of its vegetation (e.g. grassland and savanna vegetation). Fires of natural origin (caused mainly by lightning during the transition between dry and wet seasons (Ramos-Neto and Pivello, 2000) usually occur on mountaintops, in places of difficult access (ICMBio, 2007). However, they represent the minority of recorded fire outbreaks in the protected area, whose main source of fires is due to anthropogenic activities, such as the fires carried out by local residents for renovate pastures, extract plants and clear fields (ICMBio, 2007). Although fire is a vital natural disturbance for the dynamics of ecosystems such as the CDPN (Durigan, 2020), its occurrence in inappropriate places, seasons and level of intensity can cause drastic effects on biodiversity (Pivello et al., 2021).

2.2. Anuran surveys

We carefully selected sampling sites based on the presence of a water body, due to the high dependence on water for frog physiology and reproduction. We were able to sample 26 sites, maintaining a minimum distance of 1 Km between them, which were surveyed twice (January 2019 and February-March 2020) by two people. Frogs were detected using the nocturnal acoustic and visual encounter method, which is widely recognized as one of the best techniques for assessing frog species richness and abundance in tropical areas, as it allows a detailed sweep of all available environments at the sampling site (Almeida-Gomes and Rocha, 2014)). At each site, we established a 100-meter transect (bordering the water body) and spent 30 min between 19:00 and 24:00 h along the transect. Thus, our total sampling effort was 26 h (26 sites x 60 min). The collected individuals were killed in a saturated solution of Benzocaine and then fixed in 10% Formaldehyde. Finally, all specimens were preserved in 70% ethanol and deposited at the Museum of Zoology of the State University of Santa Cruz (MZUESC). All frog samplings were carried out under the environmental license number 62179-1 granted by the Ministry of the Environment (MMA), an environmental agency of the Brazilian government.

2.3. Taxonomic and phylogenetic diversity metrics

The taxonomic diversity of anuran communities was estimated through species richness, which refers to the observed species at each site. To measure phylogenetic diversity, we first constructed the phylogenetic trees of CDNP anuran communities using the time-calibrated phylogenetic tree proposed by Jetz and Pyron (2018), obtained from the VertLife database (www.vertlife.org). This tree contains phylogenetic relationships and divergence times for almost all known amphibians, encompassing a total of 7238 species (Jetz and Pyron, 2018). We pruned this tree to include only the species sampled in CDPN (see Fig. S1). Only a single species was not represented in this phylogeny (*Scinax montivagus*), and was therefore replaced by a congeneric species (*Scinax acuminatus*). For each site, we further calculated six phylogenetic metrics widely used to quantify phylogenetic diversity dimension across ecological studies (Tucher et al., 2016): one metric of phylogenetic richness (Faith's phylogenetic diversity), two metrics of phylogenetic divergence (Mean phylogenetic distance, and Mean nearest taxon phylogenetic distance) and three metrics of phylogenetic structure (standardized effect size (ses) of Phylogenetic diversity, ses Mean phylogenetic distance, and ses Mean nearest taxon phylogenetic distance).

Specifically, Faith's phylogenetic diversity represents the sum of the lengths of all branches of the phylogenetic tree of a community (Faith, 1992). Mean phylogenetic distance describes the mean phylogenetic distance (in millions of years) between all combinations of species pairs within a sample, and Mean nearest taxon phylogenetic distance measures the mean phylogenetic distance to each species closest relative in a sample (Webb, 2000). The standardized effect size of the metrics (ses) were obtained through comparisons between the values of the phylogenetic metrics observed for each sampled assemblage and the values randomly estimated after 999 generations of null communities. The null communities were generated based on the randomization of the identity of each species that occurs at each site, while maintaining the richness and abundance of species and thus assuming that all anuran species in the regional pool have the same chance of occurring in the 26 sites (Swenson, 2014). Positive ses values indicate phylogenetic evenness or overdispersion, i.e., greater phylogenetic distance between co-occurring species than expected, while negative ses values indicate phylogenetic clustering and small phylogenetic distances between co-occurring species (Kembel et al., 2009). The mean phylogenetic distance and mean nearest taxon phylogenetic distance metrics and their standardized equivalents were weighted by species abundance. The tree and all phylogenetic metrics were generated using the *phytools* (Revell, 2012) and *PICANTE* (Kembel et al., 2020) packages, respectively in R 4.2.0 software (R Core Team, 2022).

2.4. Landscape and local predictors

We extracted both local and landscape environmental variables. At the local scale (i.e., along the 100-meter transect), we measured three variables that characterize the water bodies sampled (Table 1), that are considered important for the occurrence and survival of frog species due to the ecophysiological requirements of this group (Well, 2007): water body width, water body depth and types of water body margin. The water body width and depth were quantified at five points along the 100-meter transect, which enabled us to obtain a mean that was subsequently used in the analyses. The types of margin were measured using a grid (1 x 1 m) containing 100 squares (10 x 10 cm), which were also positioned at the five points of the transect. We counted the number of squares that was almost entirely covered by each type of margin: ravine, sloping, plane and excavated. Subsequently, we used the mean coverage (in percentage) of each margin type to calculate an evenness index as a proxy for the heterogeneity of the margin of each water body sampled. For this, we used the *index_evenness* function of the *tabula* package (Frerebeau, 2022). This index informs the degree of equity of the margin, where values close to 1 denote high equitability, that is, all types of margin are observed with similar frequency, indicating a high heterogeneity of the margin in the water body in question.

We also adopted multi-scale analysis to identify the spatial scale at which the relationships between biological responses and environmental predictors are strongest ("scale of effect", Jackson and Fahrig, 2015). Based on previous studies, we selected three buffer sizes:100 (defined as the "local landscape" by Fahrig, 2013), 300 and 500 meters. In general, these scales represent the minimum, mean and maximum expectations of amphibians' dispersal abilities (Ficetola et al., 2009; Almeida-Gomes et al., 2016b). In particular, we extracted five environmental predictors at the landscape-scale (within the buffers around the sites) (Table 1): three metrics that characterize the CDPN fire regime: the burned area cover, the fire count (as a proxy for the fire frequency) and the time since the last fire (Table 1) and two related to environmental features. These metrics related to fire regime were generated based on the reconstruction of the CNPD fire history from 1990 to 2019 (see Anjos et al., 2022). In summary, a total of 30 annual vector maps were produced, each containing all the fire scars that occurred within the CDNP in each year of the time series. Then, we converted the annual vector maps into a time series of binary raster maps of the annual burned area and then, from the individually mapped fire scars and the consolidated annual maps of the burned area, we generated these metrics. In addition, we calculated the tree canopy cover, using data for 2015 derived from the Global Forest Cover Change (GFCC) Tree Cover Multi-Year Global 30 m (Sexton et al., 2013). We choose the GFCC tree cover dataset because it was the most recent satellite product available with a 30 m spatial resolution, which could give more accurate measurements of tree cover compared to the MODIS products (500 m of spatial resolution) and is also the closest date available from the end of the fire history reconstruction. We also extracted the water body cover, using the hydrographic map of the state of Bahia, derived from 5 m resolution RapidEye$^{©}$ imagery acquired for the year 2013 for the High Resolution Mapping of Brazilian Biomes Project, carried out by the Brazilian Foundation for Sustainable Development (FBDS, 2018). We selected the FBDS hydrography dataset because it is current the most detailed watercourse mapping available for our study area. All environmental predictors were extracted using the *LecoS* complement (Jung, 2015) and *raster* packages (Hijmans, 2021) in QGIS (QGIS Development Team, 2009) and R software, respectively.

Table 1. Description of each environmental predictor at local and landscape level considered in this study.

Predictor	**Description**	**Range (mean ± SD)**
Local		
Water body width (m)	Mean width of the water body sampled at each site	0 – 19.17 (4.23 ± 3.95)
Water body depth (m)	Mean depth of the water body sampled at each site	0.04 – 1.07 (0.32 ± 0.23)
Water body margin heterogeneity	Evenness diversity index (-1 to 1). Expresses how equitable is the margin of each sampled water body	0.031 – 0.96 (0.80 ± 0.18)
Landscape		
Burned area cover (%)	Percentage of the buffer covered by burned area (area of all fire scars that occurred between 2015 and 2019)	100 m scale: 0 – 100 (35.11 ± 43.33) 300 m scale: 0 – 100 (39.45 ± 39.60) 500 m scale: 0 – 100 (42.27 ± 34.99)
Fire count	The mean number of times individual pixels were burned during the period 1990 to 2019	100 m scale: 0 – 3 (1.31 ± 0.89) 300 m scale: 0 – 3.21 (1.63 ± 0.74) 500 m scale: 0 – 3.20 (1.73 ± 0.75)
Time since the last fire	The mean number of years elapsed since the last fire observed for the period 1990 to 2019	100 m scale: 0 – 27 (10.61 ± 9.08) 300 m scale: 0 – 27 (12.89 ± 8.40) 500 m scale: 0 – 27 (12.15 ± 7.59)
Tree canopy cover (%)	Mean tree canopy cover within each buffer size	100 m scale: 16.97 – 46.06 (25.19 ± 6.75) 300 m scale: 16.55 – 41.55 (24.36 ± 5.54) 500 m scale: 16.41 – 38.58 (24.42 ± 4.86)
Water body cover (%)	Mean waterbody cover within each buffer size	100 m scale: 0 – 17.59 (6.78 ± 4.12) 300 m scale: 0.60 – 8.62 (3.03 ± 1.73) 500 m scale: 0.46 – 6.39 (2.27 ± 1.34)

2.5. Statistical analyses

First, we identified the scale of effect of each environmental predictor measured at the landscape-scale on the taxonomic and phylogenetic diversities through the *multfit* function (Huais, 2018). We used the Akaike Information Criterion (AIC) to measure the strength of the statistical models of each buffer size radius. The scale of the effect of each environmental predictor varied between the different diversity metrics (see Table S1). We further evaluated the multicollinearity between all environmental predictors using the variance inflation factor (VIF) through the *vif* function of the *car* package (Fox and Weisberg, 2019). The environmental predictors moderately correlated (VIF ≥ 3) were removed from the final analyses (Dormann et al., 2013). We excluded water body width for all metrics, except ses Faith's phylogenetic diversity and Mean phylogenetic distance. In addition, we calculated the Pearson's correlation between all diversity metrics (Table S2) and found that species richness was strongly correlated only with Faith's phylogenetic diversity ($r = 0.95$, $p = 0.001$). However, the calculation of standardized effect size (ses) removed the influence of species richness on phylogenetic metrics, given that all standardized metrics are not significantly correlated with species richness (Table S2), and therefore all metrics of diversity were used in the final analyses.

We analyzed the effects of environmental predictors on each diversity metric through Generalized Linear Models (GLMs), using the *glm* function of the *stats* package (R Core Team, 2022). We first checked the distributions of all response variables using the *fitDist* function of the *gamlss* package (Rigby and Stasinopoulos, 2005). Specifically, we used the Poisson distribution for species richness, whose under and overdispersion was evaluated through dispersion tests of the *DHARMa* package (Hartig, 2022), Inverse Gaussian distribution for ses Faith's phylogenetic diversity and Gaussian distribution for

Faith’s phylogenetic diversity, Mean phylogenetic distance, Mean nearest taxon phylogenetic distance, ses Mean phylogenetic distance and ses Mean nearest taxon phylogenetic distance. In all models we used the *scale* function of the R *base* package to homogenize the variation of the environmental predictors. After constructing the global models (model including all environmental predictors) for each diversity metric, we evaluated the spatial autocorrelation of residuals from these models using Moran’s *I* (Gittleman and Kot, 1990), through the *Moran.I* function of the *ape* package (Paradis and Schliep, 2019). We subsequently using the *dredge* function of the *MuMIn* package (Barton, 2015) for to generate all possible model combinations, from the null model (containing only the intercept) to the complete model. The models were ranked based on the lowest Akaike information criteria corrected for small sample sizes (AICc). The ΔAICc value represents the difference between the AICc of a given model and the model with the lowest AICc value. Therefore, models with ΔAICc values ≤ 2 were selected as the most parsimonious models to explain the variation across the data (Burnham and Anderson, 2002). Given the high number of parsimonious models (ΔAICc ≤ 2, Table 2) found for most diversity metrics, we applied a model averaging approach through the *model.avg* function, also from the *MuMIn* package. The model averaging calculates the average effect of each predictor variable on the subset of the most parsimonious models and determines the relative importance of each predictor given its frequency in the models and its accumulated Akaike weight (Burnham and Anderson, 2002). Finally, we plotted only the relationships between the diversity metrics and environmental predictors that showed high relative importance (sum of weights ≥ 0.5) within the subset of more parsimonious models. All statistical analyzes were performed in R software 4.2.0 (R Core Team, 2022).

3. Results

We recorded a total of 448 individuals from 23 anuran species belonging to 4 families (Table 2). However, three species were excluded from the analyses because they constitute new species, i.e., they are currently in the process of description and therefore lack information about their phylogenies (Table S3). The most abundant species were *Bokermannohyla oxente* (21.20%), *Scinax montivagus* (18.75%), *Scinax curicica* (11.83%) and *Scinax machadoi* (11.60%), whereas the rarest species were *Leptodactylus fuscus*, *Leptodactylus troglodytes* and *Physalaemus cuvieri*, all representing 0.22% of the total abundance.

Table 2. List of anuran species recorded in Chapada Diamantina National Park through nocturnal acoustic and visual encounter method. Red species were not included in the analyzes and the blue species was replaced by a congeneric species (see methodology).

Species	**Family**
Boana albopunctata	Hylidae
Bokermannohyla diamantina	Hylidae
Bokermannohyla itapoty	Hylidae
Bokermannohyla juiju	Hylidae
Bokermannohyla oxente	Hylidae
Dendropsophus branneri	Hylidae
Dendropsophus minutus	Hylidae
Dendropsophus nanus	Hylidae
Haddadus aramunha	Craugastoridae
Leptodactylus fuscus	Leptodactylidae
Leptodactylus latrans	Leptodactylidae
Leptodactylus oreomantis	Leptodactylidae
Leptodactylus troglodytes	Leptodactylidae
Physalaemus cuvieri	Leptodactylidae
Proceratophrys minuta	Odontophrynidae

Proceratophrys sp1	Odontophrynidae
Proceratophrys sp2	Odontophrynidae
Proceratophrys sp3	Odontophrynidae
Rupirana cardosoi	Leptodactylidae
Scinax curicica	Hylidae
Scinax montivagus	Hylidae
Scinax machadoi	Hylidae
Scinax x-signatus	Hylidae

The mean anuran species richness among the sampling sites at the CDNP was 2.7 species (± 1.60), ranging from 1 to 10. The mean of Faith's phylogenetic diversity was 229.9 million years (± 94.35). For phylogenetic divergence, Mean phylogenetic distance was 66.36 million years (± 29.44), Mean nearest taxon phylogenetic distance was 131.91 million years (± 38.79). Regarding the phylogenetic structure, the mean values of ses Faith's phylogenetic diversity was -0.33 (± 0.91), ses Mean phylogenetic distance was -0.42 (± 0.80) and ses Mean nearest taxon phylogenetic distance was -0.47 (± 0.90).

Our best models (ΔAICc $\leq$ 2.00) indicated that the local and landscape environmental predictors distinctly influenced the taxonomic and phylogenetic diversity of anuran communities (Table 3). Two fire regime parameters (fire count and burned area cover) were more important than the other environmental predictors to explain the variation in taxonomic and phylogenetic richness (Fig. 2). We observed that the increase in fire count led to a slight increase in both species richness and Faith's phylogenetic diversity (Fig. 3b, e), while the increase of the burned area cover caused a slight decline in these diversity measures (Fig. 3c).

Table 3. Top-ranked candidate models (ΔAICc < 2) explaining the diversity patterns of anuran communities in Chapada Diamantina National Park. d.f. = degrees of freedom; AICc = Akaike Information Criteria; ΔAICc = difference between a given model and the best model; ωAICc = the model Akaike weights.

Diversity metric	Model	d.f	AICc	ΔAICc	ωAICc
Species richness	Fire count	2	91.99	0.00	0.15
	Burned cover + Fire count	3	92.25	0.25	0.13
	Null model	1	92.34	0.35	0.12
Faith's phylogenetic diversity	Fire count	3	300.28	0.00	0.45
	Bunerd cover + Fire count	4	301.07	0.78	0.30
	Fire count + Water body depth	4	301.58	1.29	0.23
Mean phylogenetic distance	Water body cover	3	232.89	0.00	0.34
	Water body cover + Water body width	4	233.67	0.77	0.23
	Fire count + Water body cover	4	233.72	0.82	0.22
	Null model	2	234.01	1.11	0.19
Mean nearest taxon phylogenetic distance	Margin heterogenity + Water body depth + Time since last fire + Tree canopy cover	6	245.07	0.00	0.09
	Burned cover + Time since last fire + Tree canopy cover	5	245.08	0.00	0.09
	Margin heterogenity + Burned cover + Time since last fire + Tree canopy cover	6	245.12	0.04	0.09
	Margin heterogenity + Burned cover + Water body depth + Time since last fire +Tree canopy cover	7	245.17	0.09	0.09

	Burned cover + Tree canopy cover	4	245.21	0.14	0.08
	Margin heterogenity + Water body depth + Time since last fire	5	245.32	0.24	0.03
	Fire count + Tree canopy cover	4	245.78	0.70	0.06
	Margin heterogenity + Water bod depth + Tree canopy cover	5	246.14	1.07	0.05
	Tree canopy cover	3	246.29	1.22	0.05
	Margin heterogenity + Tree canopy cover	4	246.54	1.46	0.04
	Margin heterogenity + Fire count + Tree canopy cover	5	246.54	1.46	0.04
	Margin heterogenity + Burned cover + Tree canopy cover	5	246.79	1.71	0.04
	Margin heterogenity + Water body cover + Tree canopy cover	5	246.82	1.74	0.04
	Burned cover + Fire count + Tree canopy cover	5	246.93	1.86	0.03
	Margin heterogenity + Time since last fire + Tree canopy cover	5	247.00	1.93	0.03
	Water body cover + Tree canopy cover	4	247.03	1.96	0.03
Ses Faith’s phylogenetic diversity	Margin heterogenity + Water body depth + Time since last fire + Tree canopy cover	6	69.06	0.00	0.12
	Margin heterogenity + Water body depth + Tree canopy cover	5	69.25	0.19	0.11
	Margin heterogenity + Water body depth + Time since last fire	5	69.31	0.24	0.11
	Margin heterogenity + FC + TCC	5	69.63	0.56	0.09
	Fire count + Tree canopy cover	4	70.32	1.25	0.06
	Margin heterogenity + Water body cover + Tree canopy cover	5	70.33	1.26	0.06
	Margin heterogenity + Water body depth + Fire count + Tree canopy cover	6	70.47	1.41	0.06
	Burned cover + Tree canopy cover	4	70.60	1.53	0.06
	Margin heterogenity + Tree canopy cover	4	70.65	1.58	0.05
	Margin heterogenity + Fire count + Water body cover + Tree canopy cover	6	70.67	1.60	0.05

	Margin heterogenity + Water body depth + Water body cover + Time since last fire + Tree canopy cover	7	70.67	1.61	0.05
	Margin heterogenity + Water body depth + Water body cover + Tree canopy cover	6	70.71	1.65	0.05
	Margin heterogenity + Water body depth + Water body cover + Time since last fire	6	70.75	1.68	0.05
ses Mean phylogenetic distance	Margin heterogenity + Fire count + Time since last fire	5	50.47	0.00	0.47
	Margin heterogenity + Fire count + Time since last fire + Tree canopy cover	6	50.21	0.74	0.32
	Margin heterogenity + Burned cover + Time since last fire +Tree canopy cover	6	52.21	1.73	0.19
ses Mean nearest taxon phylogenetic distance	Margin heterogenity + Burned cover + Time since last fire + Tree canopy cover	6	60.04	0.00	0.21
	Margin heterogenity + Fire count + Tree canopy cover	5	60.23	0.19	0.19
	Margin heterogenity + Burned cover + Water body depth + Time since last fire + Tree canopy cover	7	60.77	0.73	0.15
	Margin heterogenity + Fire count + Water body cover + Tree canopy cover	6	61.17	1.13	0.12
	Margin heterogenity + Fire count + Time since last fire + Tree canopy cover	6	61.38	1.34	0.11
	Margin heterogenity + Burned cover + Water body cover + Time since last fire + Tree canopy cover	7	61.44	1.40	0.10
	Margin heterogenity + Burned cover + Fire count + Time since last fire + Tree canope cover	7	61.64	1.60	0.09

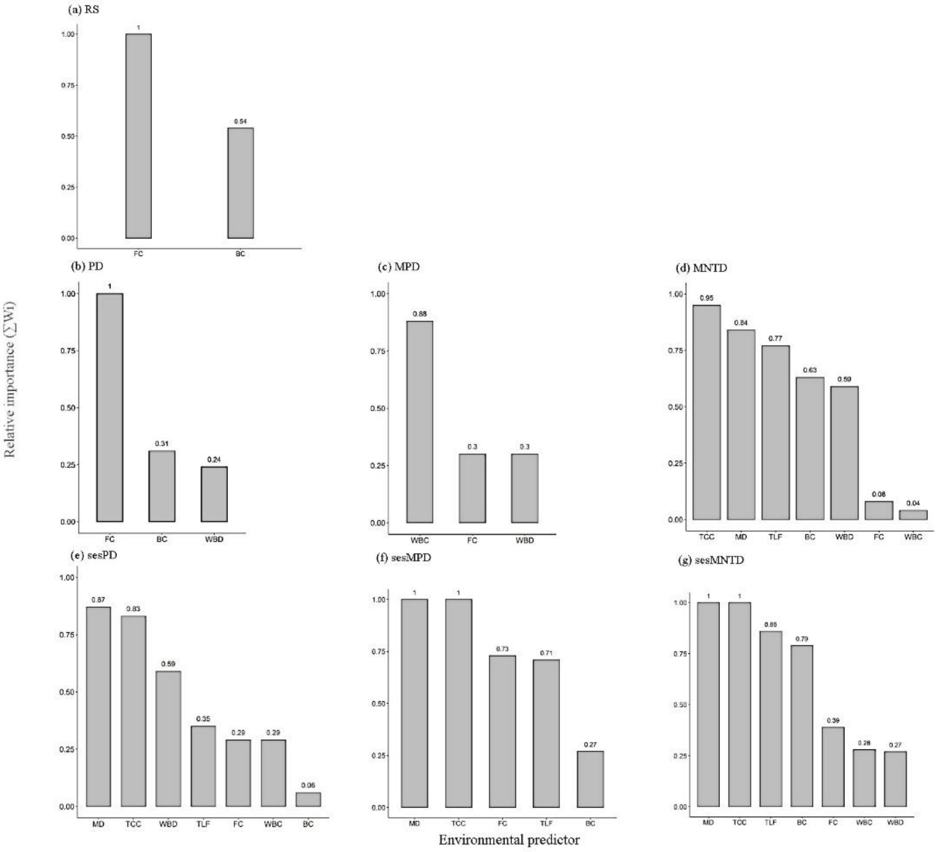

Figure 2. Relative importance of each environmental predictor within the set of more parsimonious models. ∑ωi = sum of Akaike weights. SR = species richness, PD = phylogenetic diversity, MPD = mean phylogenetic distance, MNTD = mean nearest taxon phylogenetic distance, sesPD = standardized phylogenetic diversity, sesMPD = standardized mean phylogenetic distance, sesMNTD = standardized mean nearest taxon phylogenetic distance, BC = burned area cover, FC = fire count, TLF = time since the last fire, WBC = water body cover, TCC = tree canopy cover, WBC = water body cover, WBW = water body width, WBD = water body depth, MD = margin diversity.

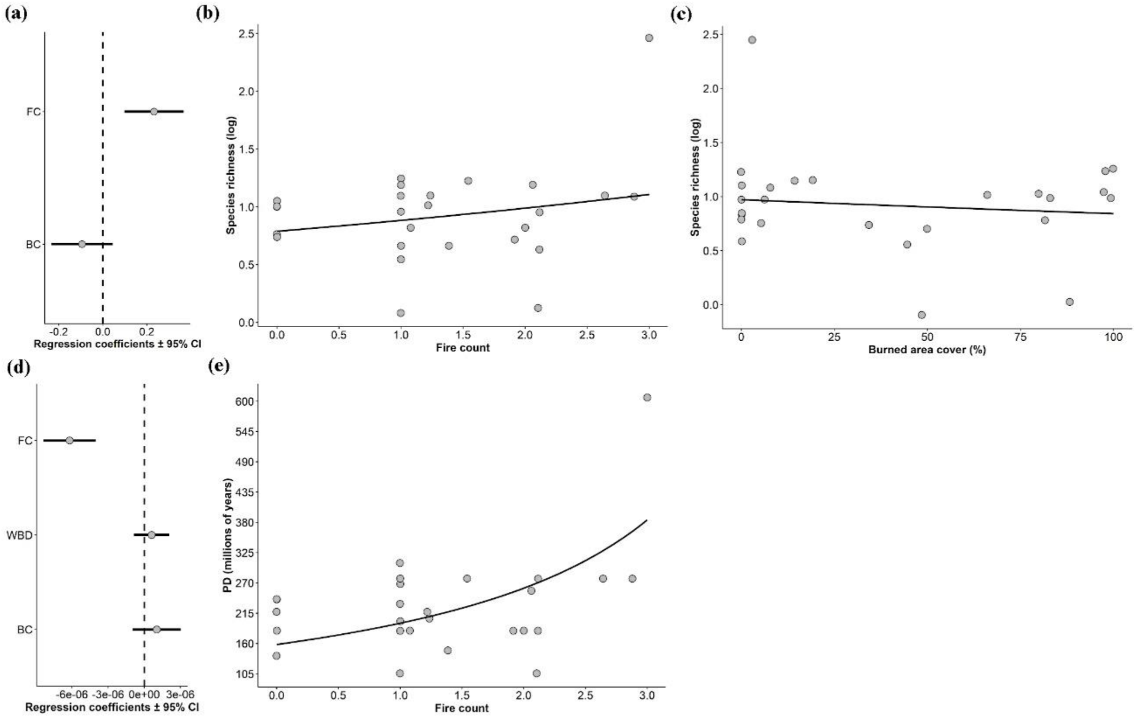

Figure 3. Relationship between the most important environmental predictors and taxonomic and phylogenetic richness. (a) and (d) result of the model averaging procedure, with coefficient estimates ± 95% confidence intervals, showing the magnitude and direction of the effect of the environmental predictors included in the set of more parsimonious models. Relationship between species richness and (b) fire count and (c) burned area cover. (e) Relationship between phylogenetic richness (PD) and fire count.

In terms of phylogenetic divergence, four models were included in the most parsimonious set to explaining the variation in mean phylogenetic distance of anurans communities (Table 3), with the water body cover comprising the most important predictor (∑ωi = 0.88, fig. 2c), affecting negatively the mean phylogenetic distance (Fig. 4b). For mean nearest taxon phylogenetic distance, 16 models were selected as most parsimonious, including almost all environmental predictors considered in this study (Fig. 4c). However, the model averaging procedure demonstrated that tree canopy cover, margin diversity and the time since last fire are the most important predictors, positively affecting the mean nearest taxon phylogenetic distance (Fig. 4d, e, f).

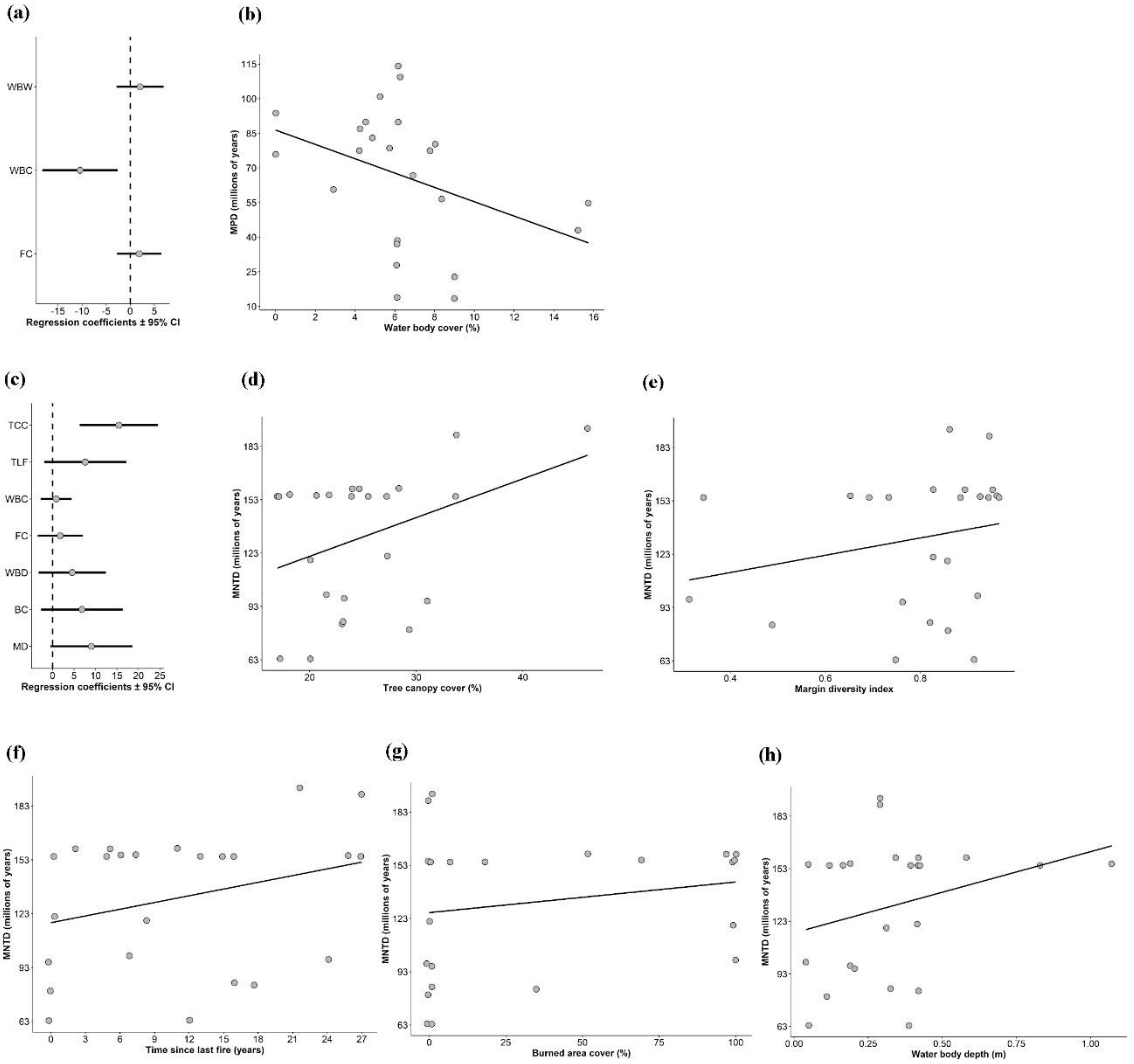

Figure 4. Relationship between the most important environmental predictors and phylogenetic divergence metrics of CDPN anuran assemblages. (a) and (c) Result of the model averaging procedure, with coefficient estimates ± 95% confidence intervals, showing the magnitude and direction of the effect of the environmental predictors included in the set of more parsimonious models. (b) Relationship between MPD and water body cover. Relationship between MNTD and (d) tree canopy cover, (e) margin diversity index, (f) time since the last fire, (g) burned area cover and (h) water body depth.

Regarding the phylogenetic structure, the most parsimonious models showed that the margin diversity and tree canopy cover are highly and equally important in explaining ses faith’s phylogenetic diversity, ses mean phylogenetic distance and ses mean nearest taxon phylogenetic distance (Fig. 2e, f, g). All the three phylogenetic metrics were positively affected by the water body margin diversity and the tree canopy cover within the landscape (Fig. 5).

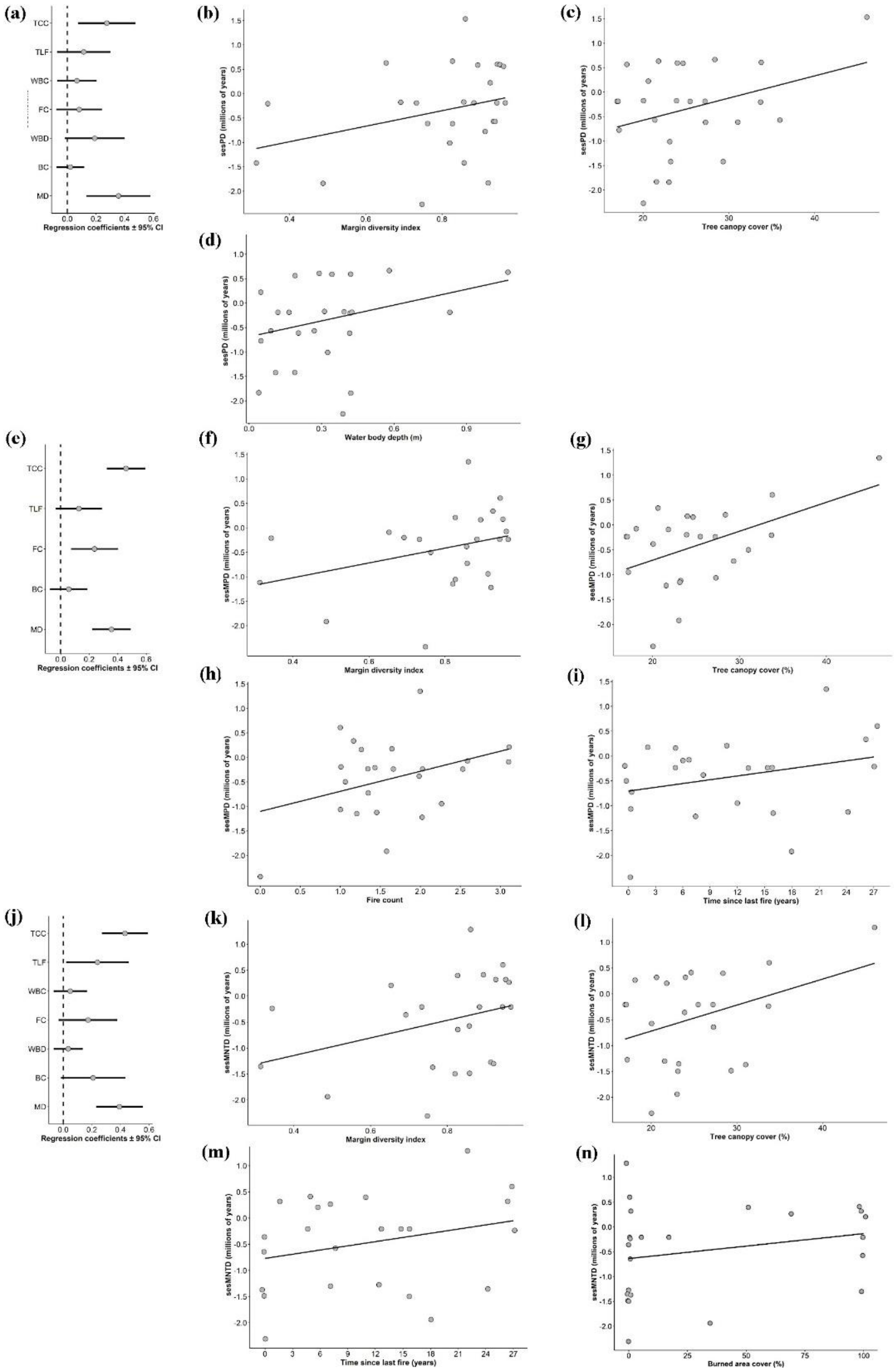

Figure 5. Relationship between the most important environmental predictors for phylogenetic divergence. (a), (c) and (j) Forest plot showing the result of the model averaging procedure, with coefficient estimates ± 95% confidence intervals, showing the magnitude and direction of the effect of the environmental predictors included in the set of more parsimonious models. Relationship between sesPD and (b) margin diversity

index, (c) tree canopy cover, (d) water body depth. Relationship between sesMPD and (f) margin diversity index, (g) tree canopy cover, (h) fire count, (i) time since last fire. Relationship between sesMNTD and (k) margin diversity index, (l) tree canopy cover, (m) time since last fire, (n) water body cover.

4. Discussion

In the last two decades, fire ecology has attracted much attention from both the scientific community and society in general, mainly due to the increasingly common occurrence of catastrophic fire events in different regions of the world (Pivello et al., 2021). Fire-dependent ecosystems have undergone drastic changes from their natural fire regimes, especially regarding the period and duration of the fire season (Rogers et al., 2020; Conciani et al., 2021). On the other hand, ecosystems in which the action of fire is historically rare, such as tropical forests, have experienced episodes of increasingly frequent and large-scale fires (da Silva et al., 2018; Barlow et al., 2020). Given this scenario, it is urgent to understand how biodiversity has been affected by these new patterns of fire regimes triggered mainly by intense human interference in the climatic conditions and land-use changes (Kelly et al., 2020). To our knowledge, our study provided the first assessment of how properties of the fire regime can shape both the taxonomic and phylogenetic diversity of anuran communities. Overall, we demonstrate that taxonomic richness and phylogenetic richness, divergence and structure of anuran communities are influenced by different environmental predictors. However, the fire frequency, the tree canopy cover and the water body margin diversity of the landscapes proved to be the most important predictors explaining the variation for most of the diversity metrics herein considered.

Regarding the fire parameters, we found that the fire frequency (fire count) was an important predictor of species richness, Faith’s phylogenetic diversity and ses Mean phylogenetic distance. An issue that must be considered is that the sites most severely affected by fire that we were able to sample burned three times over the 30 years evaluated (1990 to 2019). This fire frequency can be considered low in relation to the maximum fire frequency that we recorded in the park (see Fig. 1). Despite this, we detected that the increase in fire frequency led to a slight increase in species richness and Faith’s phylogenetic diversity (Fig. 2) and a more pronounced increase in ses Mean phylogenetic distance (Fig. 4). Anjos and collaborators (2021) showed in their review that some studies (Drummond et al., 2018; Grundel et al., 2015; Mester et al., 2015) observed an increase in anuran richness in environments affected by fire when compared to unburned ones (not only in terms of fire frequencies, also considering other fire parameters). These studies point out that this scenario can be explained by two main issues. The first is that the herpetofauna of flammable ecosystems is adapted to the natural fire regimes of their regions, presenting characteristics and behaviors that allow the species to persist in environments frequently affected by fire. In fact, some species observed in the park have these characteristics. *Leptodactylus troglodytes* and *L. fuscus*, recorded here at sites that burned three times (see Supplementary material) are recognized as burrowing species that during the burning season can shelter in underground burrows, which are less affected by the high temperatures caused by fire (de Almeida and Arzabe, 1997; Martins, 1988). Furthermore, it has been documented that the tadpoles of *L. fuscus* and *Physalaemus cuvieri* can tolerate high water temperatures and consequently low levels of oxygen (Shinya and Neto, 1991; Eterovick and Sazima, 2000). This resistance to changes in aquatic conditions observed in the larval stage may be a crucial factor for the occurrence of these species in environments more frequently affected by fire.

The second explanation for the positive relationship observed between anuran richness and fire is the landscape mosaic resulting from low-intermediate fire frequencies in these regions. Contrary to the intense environmental homogenization caused by a high fire recurrence, intermediate frequencies can provide a greater heterogeneity of the vegetation structure and the microclimatic conditions of the environment and, thus, create a variety of niches, favoring the occurrence of species with different ecological requirements (Bixby et al., 2015). This may also explain the increase in ses Mean phylogenetic distance as a function of increasing fire frequency (Fig. 4). The positive and higher values of ses Mean phylogenetic distance observed in communities inserted in landscapes with moderate fire recurrence indicate that the anuran species of these communities are less closely related. The greater variety of niches provided by the intermediate fire recurrence may have promoted the co-occurrence of species with different ecological characteristics and requirements, thus promoting the phylogenetic overdispersion in these communities.

Studies that investigate the influence of fire on phylogenetic diversity of communities of other taxa, such as plants and microorganisms, generally expect that this disturbance promotes a phylogenetic grouping in communities (Silva and Batalha, 2010; Cianciaruso et al., 2012; Rincón et al., 2013; Pérez-Valera et al., 2018). Because the fire can act as an important environmental filter, selecting those species that persist within the community based on their tolerance to the environmental conditions it triggers (e.g. the hard-coating seeds of certain plant families), it is common to record a set of phylogenetically close species (Verdú and Pausas, 2007). However, contrary to these expectations, the authors also observed that intermediate-high fire frequencies provided phylogenetic overdispersion in the evaluated communities. Silva and Batalha (2010) point out that the phylogenetic superdispersion observed in plant communities of six Brazilian savannas is mainly due to the convergence of functional traits in different plant lineages, such as the ability to resprout, which is present in more than 90% of species from Brazilian savannas. Thus, the occurrence of a large number of species able to resprout, but belonging to different plant lineages, can prevent fire from gathering closely related plants. Nevertheless, we did not find any example with anuran amphibians in the literature and although this possibility exists, we believe it is not the most plausible explanation for the positive relationship between ses Mean phylogenetic distance and the fire frequency observed in the CDNP, mainly due to the high conservatism of traits generally observed among amphibian lineages (Lourenço-de-Morais et al., 2019).

We found that the variation of ses Faith's phylogenetic diversity, ses Mean phylogenetic distance and ses Mean nearest taxon phylogenetic distance is best explained by tree canopy cover measured at the local-landscape scale (i.e., buffer of 100 m). We observed an increase in these metrics as the tree cover increased, indicating a phylogenetic overdispersion in anuran communities inserted in landscapes with greater tree cover. At CDPN, tree canopy cover values below 40% generally refer to more open vegetation, such as grasslands ("Campo Limpo") and rocky fields ("Campos Rupestres"), while values above 40% refer to formations forested areas, such as "Cerrado sensu stricto", "Floresta Estacional" and forest formations associated with water bodies, such as gallery forests. The more closed areas tend to present microhabitats with more stable temperature and humidity levels (Clewell and Aronson, 2013). It is known that the conditions of humidity and temperature of the environment are extremely important for the ecophysiology of frogs, especially for reproduction (Duellman and Trueb, 1986). The more stable microclimatic conditions of more forested areas can favor the occurrence of species with strict habitat requirements (Riós-López and Aide, 2007), in addition to promoting the permanence of generalist species that are tolerant to greater variations in conditions microclimates. This can be seen in our study by recording *Haddadus aramunha* in two sites, both with tree cover greater than 40% (see Supplementary

Material). Although this species inhabits rocky fields, it is associated with gallery forests inserted within this vegetation formation. *H. aramunha* presents direct development of terrestrial eggs (Cassimiro et al., 2008) and this characteristic makes it less independent of aquatic environments while more dependent on moist soils for oviposition. In this way, the condition of high soil moisture, generally guaranteed in more closed environments, can reduce the risks of dissection of eggs of this species. In addition to providing microhabitats with more stable temperature and humidity levels, the higher density of shrubs and trees present in more closed environments can favor the segregation of arboreal species that use vertical call sites, which reduces physical confrontations and agonistic interactions in the dispute over females and calling sites (Gonçalves et al., 2015), thus allowing the co-occurrence of distinct tree species (e.g. different species of the genus *Bokermannohyla*) and promoting phylogenetic dispersion in communities inserted in these landscapes with greater tree cover.

Lastly, we identified that the water body margin heterogeneity is also a determinant predictor of the phylogenetic structure of CDPN anuran communities, where the highest values of ses faith’s phylogenetic diversity, ses mean phylogenetic distance and ses mean nearest taxon phylogenetic distance observed were in sites with high values margin diversity index (Fig. 4). It is important to note that the margin diversity was the only local environmental predictor with high relative importance in the explanation of these metrics (Fig. 5). Although little investigated and tested, the margin configuration (slope angle, shape and type of vegetation present on the margin) is associated with adult reproductive habits as well as for the development of tadpoles (Wells, 2007). Water bodies with greater margin heterogeneity allow different lineages to use it as a calling and oviposition sites, in addition to promoting a wide variety of refuges for tadpoles of different species (Guderyahn et al., 2016), thus contributing to greater phylogenetic diversity of these communities.

5. Conclusions

Intense man-made changes in natural fire regimes are considered one of the main threats to biodiversity in the Anthropocene (Malhi et al., 2014), which makes understanding how fire disturbances shape facets of biodiversity urgent, especially for organisms more vulnerable to fires, such as frogs. We demonstrated that the variation in taxonomic diversity of anuran communities was explained only by fire parameters, while phylogenetic diversity was best explained by landscape-scale environmental predictors. This indicates that environmental characteristics can influence the facet of anuran diversity in different ways and that the evaluation of a single facet of diversity can lead to wrong conclusions and, consequently, to failed conservation plans and actions. Although we were unable to investigate functional diversity due to limitations in our dataset, we reinforce the importance of including all facets of diversity to better understand how fire and local and landscape environmental features structure the diversity of faunal communities in natural ecosystems. In addition, we emphasize that intermediate fire frequencies can promote a high taxonomic and phylogenetic diversity and therefore adequate fire management is essential to maintain the diversity of anurans in this complex Brazilian protection area. Finally, we demonstrate the importance in maintaining native tree cover to maintaining anuran diversity in the studied flammable system.

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SUPLEMENTARY MATERIAL

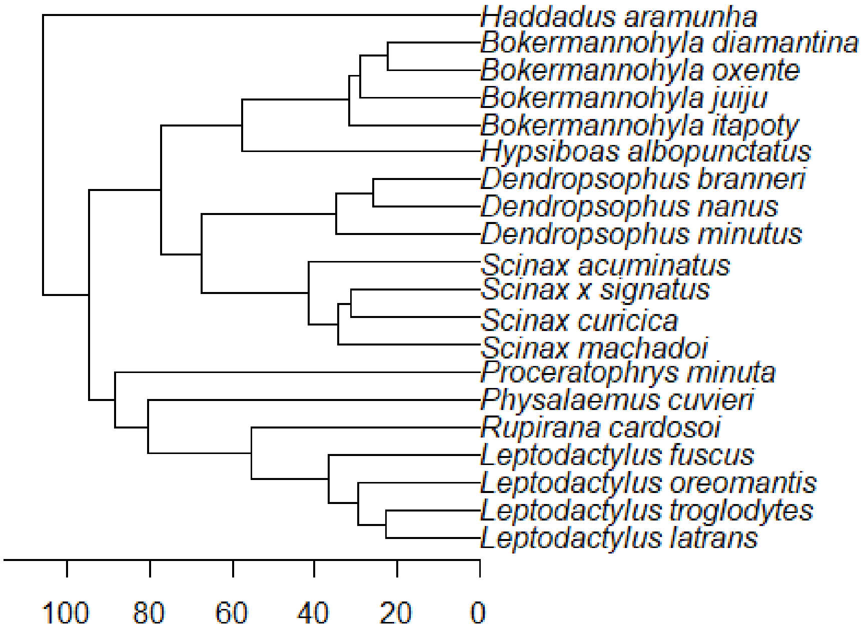

Figure S1. Community phylogeny (n = 20 species) showing the species sampled at the Chapada Diamantina National Park. The axis below the figure represents the time in millions of years since present day.

Table S1. Scale of effect (meters) for each landscape-scale environmental predictor used in the study. SR = species richness, PD = phylogenetic diversity, MPD = mean phylogenetic distance, MNTD = mean nearest taxon phylogenetic distance, sesPD = standardized phylogenetic diversity, sesMPD = standardized mean phylogenetic distance, sesMNTD = standardized mean nearest taxon phylogenetic distance, BC = burned area cover, FC = fire count, TLF = time since the last fire, WBC = water body cover, TCC = tree canopy cover.

Diversity metric	**BC**	**FC**	**TLF**	**WBC**	**TCC**
SR	300	100	500	500	100
PD	300	100	100	300	100
MPD	100	300	100	100	100
MNTD	100	500	100	500	100
sesPD	500	300	100	500	100
sesMPD	100	500	100	500	100
sesMNTD	100	500	100	500	100

Table S2. Pearson's correlation between the diversity metrics considered in this study. The values below the diagonal are the correlation values. Values above the diagonal are P-values, with those highlighted in bold representing significantly strong correlations.

	SR	PD	MPD	MNTD	sesPD	sesMPD	sesMNTD
SR		**<0.001**	0.01	1.00	1.00	1.00	1.00
PD	0.95		**0.001**	1.00	1.00	1.00	1.00
MPD	0.45	0.56		1.00	1.00	1.00	1.00
MNTD	0.39	-0.13	0.11		**<0.001**	**<0.001**	**<0.001**
sesPD	-0.01	0.26	0.32	0.88		**<0.001**	**<0.001**
sesMPD	-0.08	0.19	0.37	0.87	0.93		**<0.001**
sesMNTD	-0.14	0.14	0.28	0.95	0.96	0.94	

CONCLUSÃO GERAL

Os resultados gerados nesta tese ampliam o conhecimento acerca dos efeitos das queimadas sobre os anfíbios anuros, uma temática ainda pouco investigada em âmbito global. Através do primeiro capítulo demonstramos como diferentes atributos biológicos dos anuros podem ser influenciados por distintos parâmetros do fogo. Prenchemos algumas lacunas sobre como os estudos relacionados a este tema tem sindo desenvolvidos e a partir das análises dos dados levantados, realizamos recomendações principalmente para o delinemanento das futuras pesquisas. Em particular, sugerimos que os estudos adotem sempre que possível, um delineamento de médio a longo prazo para garantir que os principais impactos do fogo sejam detectados. Bem como, um delineamento do tipo “Antes e depois” do evento de queima com a finalide de compreender a situação prévia das comunidades e das condições ambientais anteriores ao fogo. Além disso, recomendamos a utilização de parâmetros que melhor caracterizam o evento de queima, como a quantidade de área queimada, o intervalo, frequencia e severidade de fogo e que os efeitos destes parâmetros sejam também investigados sobre outras facetas da diversidade de anuros como a diversidade funcional e filogenética.

Por meio do segundo capítulo revelamos como fatores ambientais atuando em distintas escalas espaciais podem afetar importantes propriedades do regime de fogo do Parque Nacional da Chapada Diamantina, um ecossistema savanico brasileiro. Através dos resultados gerados, sugerimos medidas para auxiliar em um manejo do fogo mais adequado para a conservação dos ecossistemas desta unidade de conservação. Recomendamos por exemplo, que as atividades de monitoramento de incêndios do PNCD sejam reforçadas em paisagens localizadas na região oeste do parque, em altitudes acima de 600 metros, e que apresentam a predominância de formações vegetais campestres, como o Campo Limpo e Campo Rupestre. Além disso, em virtude dos incêndios mais recentes (de 2005 a 2019) terem afetado maiores áreas do parque em comparação com os incêndios mais antigos (de 1990 a 2004), alertamos que a política de supressão máxima do fogo, até entao adotada no parque, pode não ser apropriado para os ecossistemas existentes nesta regiao e que o manejo integrado do fogo (MIF) configuraria uma estratégia de manejo mais adequada tanto para a conservação do parque quanto para as comunidades locais.

Por fim, através do último capítulo fornecemos a primeira avaliação de como as propriedades do regime de fogo e características ambientais locais e de paisagem podem moldar a diversidade taxonômica e filogenética das assembleias de anuros. Revelamos que estes preditores ambientais influenciam de maneiras distintas as facetas da diversidade de anuros e que considerar uma única faceta da diversidade pode nos levar a conclusões equivocadas e potencialmente a planos e ações de conservação inadequados. Demonstramos que para assegurar uma elevada diversidade taxonômica e filogenética de anuros, é necessário presevar os ambientes com maior cobertura arbórea, como áreas de Cerrado stricto sensu e de Matas de galeria. Além de promover ações de manejo de fogo que possibilitem uma baixa a intermediária frequência de queima, tendo em vista que ambos os fatores proporcionam uma maior heterogeneidade de nichos, possibilitando assim, uma maior coocorrencia de espécies ecologicamente distintas nas paisagens do parque.