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FIRES IN THE ATLANTIC FOREST: SELECTIVITY TOWARDS DIFFERENT ENVIRONMENTS AND IMPACTS ON BIRD DIVERSITY

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Fires in the Atlantic Forest: Selectivity towards different environments and impacts on bird diversity

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Dedico este trabalho à minha família

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Eu sou o que me cerca. Se eu não me preservar o que me cerca, eu não me preservo.

José Ortega y Gasset

Resumo

Incêndios florestais têm se tornado um distúrbio cada vez mais frequente em florestas tropicais, impulsionados pela intensificação das atividades humanas e pelas mudanças climáticas. Nesse contexto, compreender os padrões de ocorrência do fogo e seus impactos nas comunidades biológicas é essencial para subsidiar estratégias de manejo e conservação. Nesta tese de doutorado, busquei abordar essas questões no bioma da Mata Atlântica por meio de dois capítulos. No primeiro capítulo, publicado na revista *Journal of Environmental Management*, investiguei como o fogo seleciona diferentes tipos de uso e cobertura da terra ao longo de um período de 35 anos (1987–2022). A análise de mais de 40.000 incêndios revelou que florestas secundárias são os ambientes mais suscetíveis ao fogo, enquanto florestas maduras apresentam a menor propensão, evidenciando sua notável resistência a incêndios. Um achado particularmente relevante foi a diminuição da seletividade do fogo em florestas secundárias ao longo do tempo. Esse resultado sugere que, à medida que o processo de sucessão ecológica avança, as florestas secundárias tornam-se progressivamente mais resistentes ao fogo. No segundo capítulo, submetido à revista *Journal of Applied Ecology*, investiguei os impactos do fogo nas comunidades de aves da Mata Atlântica. Especificamente, analisei como o fogo influencia a composição e a diversidade, tanto taxonômica quanto funcional, dessas comunidades, bem como os efeitos de características da paisagem e dos incêndios sobre essas respostas. Os resultados indicaram que, de forma geral, a composição e a diversidade das comunidades de aves não foram significativamente alteradas pelo fogo. No entanto, a riqueza de espécies mostrou uma associação positiva com a produtividade da vegetação, enquanto a diversidade funcional foi influenciada pelo tamanho dos incêndios. Em conjunto, os dois capítulos desta tese oferecem novas evidências sobre as interações entre o fogo, a paisagem e a biodiversidade na Mata Atlântica. Os resultados ressaltam a importância de políticas públicas e estratégias de manejo que considerem as particularidades locais, incluindo iniciativas de restauração florestal e práticas de manejo inteligente do fogo. Essas ações são cruciais para mitigar os impactos crescentes dos incêndios florestais e proteger a biodiversidade deste bioma extremamente ameaçado.

Palavras-chave: aves, diversidade funcional, NDVI, NBR, pastagens, severidade do fogo, tamanho do incêndio

Abstract

Wildfires are becoming an increasingly common disturbance in tropical forests, driven by the intensification of human activities and climate change. In this context, understanding fire patterns and its impacts on biological communities is critical to informing effective management and conservation strategies. This PhD thesis tackles these issues within the Atlantic Forest biome through two main chapters. In the first chapter, published in the *Journal of Environmental Management*, I explored how fire interacts with different land-use and land-cover types over a 35-year period (1987–2022). By analyzing data from more than 40,000 fires, I found that secondary forests are the most fire-prone environments, while old-growth forests are the least susceptible, demonstrating their remarkable resilience to fire. One particularly striking result was the reduced fire selectivity in secondary forests over time, suggesting that as ecological succession progresses, these forests become increasingly resistant to fire. The second chapter, submitted to the *Journal of Applied Ecology*, investigates how fire affects bird communities in the Atlantic Forest. I focused on how fire influences species composition and diversity—both taxonomic and functional—while also examining how landscape and fire characteristics shape these responses. The findings showed that, overall, fire did not significantly alter the composition or diversity of bird communities. However, species richness was positively linked to vegetation productivity, and functional diversity was influenced by fire size. Together, these two chapters provide valuable insights into the complex interactions between fire, landscapes, and biodiversity in the Atlantic Forest. The results highlight the need for public policies and management strategies that are tailored to local conditions, such as forest restoration initiatives and fire-smart management practices. These actions are essential for addressing the increasing threat of wildfires and preserving the biodiversity of this critically endangered biome.

Keywords: birds, functional diversity, NDVI, NBR, pastures, fire severity, fire size

Sumário

Introduction

The year was 2019. The news on television and the internet was always the same: Brazil was on fire. Whether in the Amazon, the Cerrado, or any other biome, the Brazilian landscapes looked identical: a gray sea with waves of smoke. Images of charred animals circulated throughout the country. Who could forget the image of a carbonized jaguar? Today, six years later, the situation remains unchanged. This scenario motivated me to work on this topic and, in some way, seek solutions to mitigate (even if modestly) this environmental issue.

This doctoral thesis, focused on the Atlantic Forest biome, pursued two primary objectives: (i) to analyze fire selectivity among different land-use and land-cover types (LULCs) and (ii) to assess the impacts of fire on bird communities. In this general introduction, I examine the history of fire in tropical forests, with a particular emphasis on Brazil, discussing its major environmental impacts and the key factors driving current fire activity. I also discuss fire impacts on birds, focusing on tropical forests. Finally, I provide an overview of the chapters developed throughout this research.

Fire history in Brazilian tropical forests

Fires are ecological disturbances with a heterogeneous global distribution across biomes. In tropical forests, fire events were historically rare, with return intervals ranging from hundreds to thousands of years, as evidenced by charcoal records (Uhl & Kauffman, 1990). This low frequency was largely attributed to the high humidity typical of these forests, which limited both fire ignition and spread (Cochrane, 2003; Cochrane et al., 1999). Until a few decades ago, the occurrence of frequent fires in tropical forests was considered unimaginable. However, the synergistic interaction between climate change and human activities has profoundly altered fire behavior (Le Page et al., 2017). Today, fire frequency has increased dramatically, with return intervals reduced to decades or even shorter periods (Cochrane, 2003). These changes not only increase the number of fires but also alter their dynamics, intensifying their extent and severity (Bowman et al., 2009).

In Brazil, fires were only recognized as a significant environmental issue in the late 1990s, spurred by growing awareness of the environmental and financial damages resulting from the historical misuse and indiscriminate application of fire (Soares et al., 2009). A landmark event during this period was the great fire in the state of Roraima in 1997 (INPE, 1998), which devastated approximately 11,000 km². This incident garnered national and international attention, marking one of the first clear indicators of how the interaction between human activities, such as deforestation and slash-and-burn practices, and climate change was reshaping fire dynamics.

Studies from that time had already warned of the rising incidence of fires in Brazil's tropical forests and the severe environmental challenges this would entail (Cochrane et al., 1999). These predictions have been alarmingly validated. In 2024, Brazil experienced nearly 280,000 fire events, with a burned area of approximately 22 million hectares (INPE, 2024; Mapbiomas, 2024). These events received extensive coverage from Brazilian media outlets, which highlighted not only the alarming scale of the fires but also their devastating impacts on fauna, flora, and ecosystem services. Reports underscored widespread biodiversity loss, increased carbon emissions, and severe threats to local communities and indigenous territories (Figure 1).

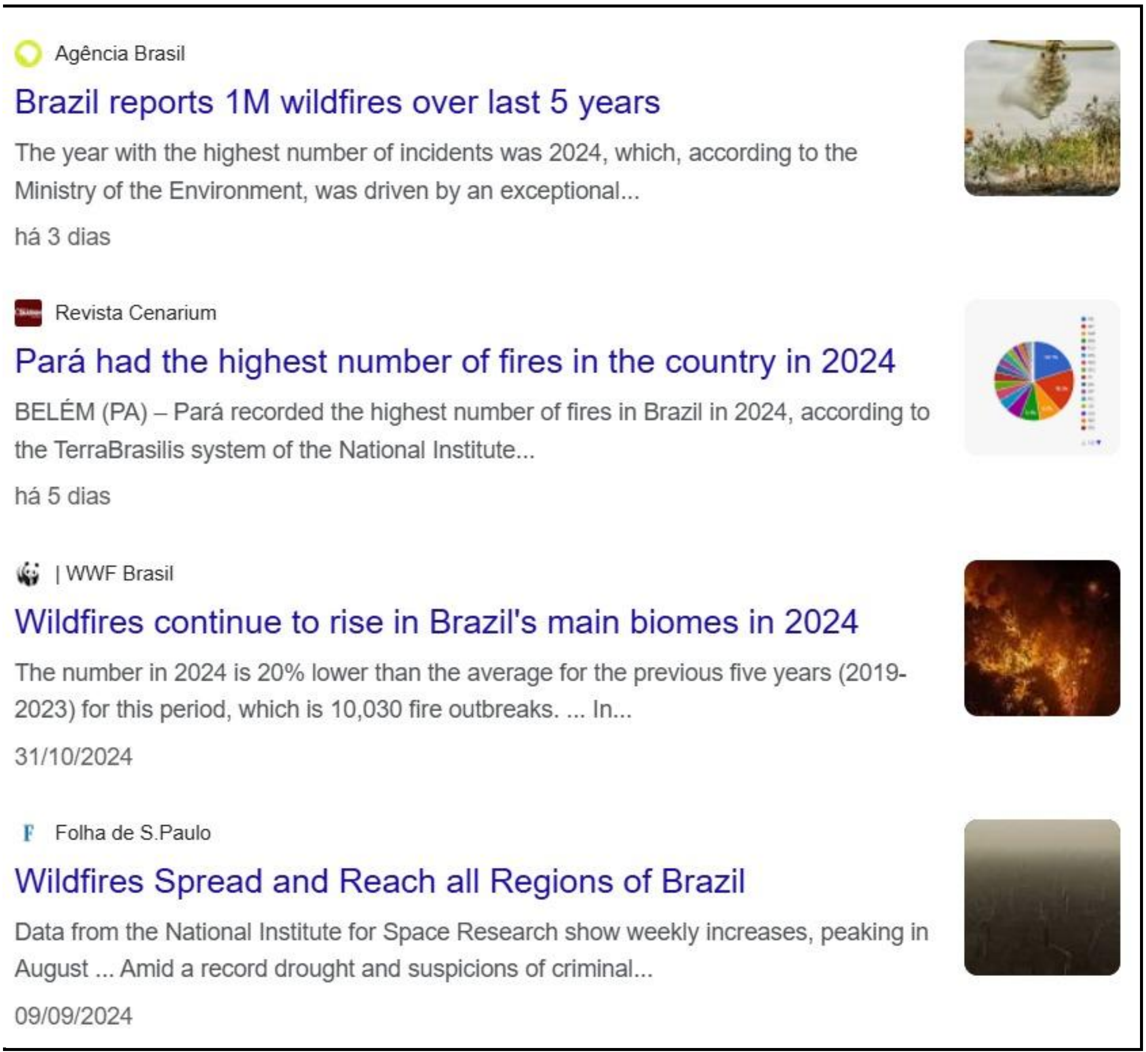

Figure 1. News reports from 2024 highlighting forest fires in Brazil. These news articles were retrieved from Google on January 13, 2025, and include: "Brazil reports 1M wildfires over last 5 years" (Agência Brasil, https://agenciabrasil.ebc.com.br/en/meio-ambiente/noticia/2025-01/brazil-reports-1m-wildfires-over-last-5-years); "State in the Amazon had the highest number of fires in Brazil in 2024" (Revista Cenarium, https://revistacenarium.com.br/en/state-in-the-amazon-had-the-highest-number-of-fires-in-brazil-in-2024/); "Wildfires continue to rise in Brazil's main biomes in 2024" (WWF Brasil, https://www.wwf.org.br/?90121/Wildfires-continue-to-rise-in-Brazils-main-biomes-in-2024); and "Wildfires spread and reach all regions of Brazil" (Folha de S.Paulo, https://www1.folha.uol.com.br/internacional/en/scienceandhealth/2024/09/wildfires-spread-and-reach-all-regions-of-brazil.shtml).

Fire impacts

In Brazil, most fires occur in agricultural landscapes, where they are intentionally set for purposes such as pest control, clearing stubble, renewing pastures, or expanding agricultural frontiers (da Silva Junior et al., 2020). Other causes of fires include the release of fire balloons, acts of arson by criminals or pyromaniacs, and natural factors like lightning strikes (Carvalho et al., 2022). These anthropogenic and natural fires often escape into adjacent forests, which lack the evolutionary adaptations to tolerate or recover from such disturbances (Pivello et al., 2021).

Forest fires typically manifest as low-intensity surface fires, burning through the dry litter layer on the forest floor. While such fires primarily affect smaller trees and seedlings, causing significant mortality in these groups (Barlow et al., 2002; Uhl & Kauffman, 1990), their impacts can escalate under extreme drought conditions. During these periods, surface fires can intensify into high-severity fires that kill larger, thin-barked trees, further degrading the forest structure and resilience (Uhl & Kauffman, 1990).

Once a forest is burned, its vulnerability to future fires increases significantly. The fragmented canopy allows for greater solar heating, altering the microclimate and facilitating the invasion of fire-adapted grass species. This creates conditions where fires become recurrent and endemic (Cochrane et al., 1999). Such altered fire dynamics often develop into a self-reinforcing cycle: each fire event exacerbates fuel accumulation on the forest floor and intensifies the severity of subsequent fires (Cochrane, 1999).

The ecological consequences of these fires are profound. They drive changes in biodiversity, often resulting in species loss or shifts in community composition (Kelly et al., 2017, 2020). Fire events also degrade soil quality (Nadporozhskaya et al., 2018), increase erosion rates (Girona-García et al., 2024), and negatively affect freshwater ecosystems, such as rivers and lakes (Vaz et al., 2014, 2021). Furthermore, fires diminish water retention capacity (Sansevero et al., 2020; Schmerbeck & Fiener, 2015) and alter landscape dynamics, with cascading effects on vegetation cover, carbon storage, and ecosystem services (Moreira et al., 2009; Silva et al., 2009).

Fire impacts do not rely only on the environment. The economic and public health impacts of fires in Brazil are profound, affecting various sectors and posing significant challenges to sustainable development. Economically, fires lead to substantial losses in gross domestic product (GDP), agricultural productivity, and ecosystem services, particularly in regions like the Pantanal and Amazon. For example, the Pantanal fires of 2019 and 2020 resulted in GDP declines of -0.79% in Mato Grosso do Sul and -0.98% in Mato Grosso, with the livestock and agricultural sectors being the most affected (Scur et al., 2023). Fires in the Amazon cause annual losses of approximately $39 ± 2 per hectare, escalating to $183 ± 30 in areas with recurrent fires (Strand et al., 2018). These losses are further exacerbated by the negative correlation between fires and agricultural outputs, particularly for key crops like soybeans and corn, which are vital to Brazil's economy (Inacio et al., 2022). Additionally, smallholders often face a fire-poverty trap, where reliance on fire-based practices reduces yields and perpetuates economic stagnation (Cammelli et al., 2020).

The public health impacts are equally severe, as fires significantly increase air pollution through the release of particulate matter (PM2.5), which has been linked to respiratory and cardiovascular diseases. During wildfire waves, hospital admissions for respiratory illnesses rise by 23%, while circulatory diseases increase by 21% (Requia et al., 2021). Fires in the Amazon in 2019 alone were responsible for approximately 3,400 additional deaths due to PM2.5 exposure (Butt et al., 2021). These health risks are exacerbated by deforestation, which not only drives fire activity but also contributes to carbon emissions and biodiversity loss, hindering long-term economic and environmental sustainability (Cammelli et al., 2020).

Drivers of fire activity

Fire behavior in tropical forests is primarily driven by human activities and climate dynamics. Among these factors, the expansion of agricultural frontiers plays a pivotal role in increasing fire activity. Agricultural practices often rely on fire as a cost-effective tool for land clearing and management, particularly in regions undergoing rapid agricultural expansion, such as the Amazon and Cerrado biomes in Brazil, as well as parts of Asia (Carlson et al., 2012; Morton et al., 2008). This process significantly alters landscape composition by replacing undisturbed forests with more flammable land use and land cover types (LULCs). In the Amazon and Atlantic Forest biomes, for example, pastures exhibit the highest fire ignition rates and frequently act as conduits for fire spread into adjacent forested areas, further exacerbating deforestation and forest degradation (Gutiérrez-Vélez et al., 2014). On the other hand, some evidence suggests that eucalyptus plantations may offer partial protection against fire. Plantation owners, motivated by the need to safeguard their investments, actively suppress and control fires that could damage their eucalyptus crops, thereby creating a fire buffer effect in certain areas (Guedes et al., 2020).

Agricultural expansion also drives changes in landscape configuration, influencing fire behavior primarily through the processes of fragmentation and the resulting edge effects. Fragmentation refers to the breaking apart of large, contiguous forested areas into smaller, isolated patches, often separated by anthropogenic LULCs (Driscoll et al., 2021). As forests are fragmented, human activities tend to increase significantly in these areas. This increased human occupation and use intensifies pressures on fragmented ecosystems, resulting in higher rates of degradation and an increased risk of forest fires (Driscoll et al., 2021).

Moreover, fragmentation amplifies edge effects—environmental changes that occur at the interface between forested areas and adjacent open or modified landscapes. Forest edges are more exposed to external factors such as wind, direct sunlight, and reduced humidity, which create microclimates that differ significantly from the forest interior. These altered conditions heighten the vulnerability of forest edges to degradation, increase tree mortality, promote the accumulation of combustible materials, and make these areas more prone to fires (Driscoll et al., 2021). Notably, previous studies have shown that up to 90% of forest fires are associated with forest edges in tropical forests (Cochrane, 2001).

Such changes in forest edges reduce the ability of tropical forests to recycle water, making them drier (Spracklen et al., 2012) and therefore more susceptible to fires. In general, both local- and large-scale climate conditions are closely linked to fire activity in tropical forests. Previous studies have documented that fire activity in these regions is associated with decreased precipitation and extended dry seasons (Aragão et al., 2018; Gutiérrez-Velez et al., 2014). Precipitation plays a crucial role in influencing wildfire occurrence, both directly and indirectly. The amount and distribution of rainfall are key factors in determining the start, duration, and end of the fire season or periods of heightened fire risk (Aragao et al., 2018). Climate change and more intense El Niño events further exacerbate this dynamic by increasing the intensity and duration of dry seasons, thereby creating conditions that significantly heighten fire activity (Aragão et al., 2018). These prolonged and severe dry periods reduce soil and vegetation moisture, facilitating fire ignition and spread while amplifying the scale and severity of wildfire events.

Fire spread in human modified landscapes

Fires can spread from a local epicenter to cover extensive areas, with their propagation rate being either enhanced or hindered by the spatial arrangement of fuel across the landscape. The amount and spatial distribution of fuel are fundamental factors in explaining fire ignition and propagation. Discontinuities in fuel loads lead to variations in fire-propagation rates (Carmo et al., 2011a). Consequently, fires play different roles across the components of landscape mosaics and at various stages of land-cover change trajectories (Eva & Lambin, 2000). This is because land-cover types are closely linked to fuel characteristics (Turner et al., 1997).

If all LULCs within a landscape were equally fire-prone, fires would occur randomly. However, research shows that certain LULCs are more susceptible to fire than others (Carmo et al., 2011; Moreira et al., 2009). The spatial arrangement of LULCs influences fire occurrence patterns, as the probability of both fire ignition and spread varies across these types (Moreira et al., 2001). For instance, in Mediterranean areas, shrublands, grasslands, and coniferous forests are more prone to fire than croplands and broadleaf forests (Oliveira et al., 2014). In Brazil, studies indicate that pastures account for the largest proportion of burned areas (Alencar et al., 2022). However, it remains unclear whether this is due to the extensive presence of pastures in the Brazilian landscape or their inherent high fire susceptibility. Understanding fire selectivity toward specific LULCs is critical for informing policy decisions, as LULCs, unlike other factors such as topography or weather, can be actively managed.

Fire impacts on birds

Fire behavior influences the distribution and abundance of species, population sizes, and the availability of critical resources such as food and shelter (Barlow & Peres, 2004; Chia, 2015; González et al., 2022). Additionally, fires can impact various ecological interactions, including competition and predation (Letnic et al., 2013). Consequently, it is expected that fires will affect bird communities. However, bird responses to fire can vary widely depending on the species, population characteristics, and locations (González et al., 2022).

Bird responses to fires can range from negative to positive (Fontaine & Kennedy, 2012). During fire events, most birds are able to escape due to their high mobility. However, nestlings, weak fliers, and ground-dwelling species may be unable to flee, making them vulnerable to the direct effects of smoke and flames, which can lead to mortality (Mardiastuti, 2020). On the other hand, some species may respond positively to fires: raptors often circle above the flames, preying on small mammals escaping the burning areas, while insectivorous birds exploit the smoke column to catch insects (Mardiastuti, 2020).

Most impacts on birds are associated with post-fire changes in vegetation. Some species are closely tied to the complex vegetation structures found in unburned areas, while others benefit from the open habitats typically created by fire (Barlow & Peres, 2004). Consequently, fires often drive shifts in species composition, replacing highly specialized and rare species with those better adapted to disturbed environments (Barlow et al., 2002; Mestre et al., 2013). These effects can persist for years, with the restructuring of bird assemblages varying by region. In the Amazon, it can take three to more than ten years for bird communities to recover after a fire (Barlow et al., 2002; Mestre et al., 2013). In contrast, tropical forests in Southeast Asia may experience a complete restructuring of bird assemblages within five years of a fire event (Adeney et al., 2006).

Variation in bird recovery is closely tied to the landscape characteristics of different regions. Native forest cover, for instance, plays a vital role in shaping bird communities during and after fires by providing ecological refuges and serving as sources for recolonization (Robinson et al., 2014; Watson et al., 2012). In contrast, vegetation productivity serves as a proxy for resource availability, influencing bird presence in burned landscapes (Leveau & Isla, 2021; Pettorelli et al., 2005). Additionally, fire characteristics—such as size and severity—are strongly linked to changes in resource availability, often disrupting post-fire occupancy patterns and affecting landscape connectivity (Parkins et al., 2018; Steel et al., 2018, 2022). Regional variations in these factors likely reflect differences in the time required for bird communities to recover after fire events.

Fires in the Atlantic Forest

The Atlantic Forest (AF) biome, one of the world's most critical biodiversity hotspots, faces severe challenges due to fire and human-induced disturbances. Historically spanning 160 million hectares across Brazil, Argentina, and Paraguay (Muylaert et al., 2018), the AF has suffered centuries of intense deforestation and land-use changes, leading to the widespread loss of old-growth forests. Today, only about 36% of its natural vegetation remains, much of it fragmented into small patches under 50 hectares, isolated, and heavily impacted by human activities (Rezende et al., 2018; Ribeiro et al., 2009; Vancine et al., 2024). These fragmented landscapes, with their exposed and drier edges, are increasingly susceptible to ignition, particularly in areas adjacent to human-modified environments (Cochrane et al., 1999).

Fire poses a particularly serious threat to this already vulnerable biome. Fragmentation and fire interact in a destructive feedback loop: recurrent fires degrade forest fragments, delaying or halting regeneration and creating conditions that favor further fire events (Cochrane et al., 1999; dos Santos et al., 2019; Driscoll et al., 2021).

This cycle can result in large-scale ecological shifts, transforming forests into non-forest ecosystems and jeopardizing the biome's unique biodiversity and resilience (dos Santos et al., 2019; Sansevero et al., 2020). Fires also disrupt the natural transition of secondary forests towards old-growth vegetation, resetting regeneration processes and potentially pushing the biome toward a savanna-like state (dos Santos et al., 2019; Sansevero et al., 2020a).

Despite these threats, conservation efforts over recent decades have led to some improvements in vegetation cover. Government policies, such as the Atlantic Forest Law (2006) and the Brazilian Forest Code (2012), along with reforestation and natural regeneration driven by agricultural abandonment and rural depopulation, have contributed to the recovery of secondary forests (Vancine et al., 2024). However, these measures have not been sufficient to address the growing role of fire in shaping the AF landscape, underscoring the urgent need for targeted strategies to mitigate fire impacts and safeguard the biome's extraordinary biodiversity.

In Brazil, fire-related research has predominantly focused on the Amazon and Cerrado biomes, leaving the Atlantic Forest relatively understudied. This knowledge gap limits our understanding of how fire behaves in the AF’s highly fragmented and human-modified landscapes, which differ significantly from the more extensive and continuous forest cover of the Amazon. The degraded state of the AF likely alters fire dynamics and their ecological consequences, highlighting the importance of investigating fire behavior and its impacts in this fire-sensitive biome.

Regarding avian communities, research on fire's effects in the AF is remarkably scarce. To date, only one study has examined the interaction between fire and birds in this biome, focusing on the sensitivity of understory species in burned versus unburned areas

(Loures-Ribeiro et al., 2011). This significant gap in knowledge underscores the urgent need for research on fire's broader ecological consequences in the Atlantic Forest, particularly given its status as one of the planet's most biodiverse and threatened ecosystems (Myers et al., 2000; Rezende et al., 2018).

Chapters of the thesis

This doctoral thesis is divided into two chapters. In the first chapter, I examined how different LULCs are selected by fire across the various ecoregions of the Atlantic Forest. To achieve this, over 40,000 fires were analyzed over a 35-year period. This chapter, titled "Relative fire-proneness of land cover types in the Brazilian Atlantic Forest," has been published in the Journal of Environmental Management (https://doi.org/10.1016/j.jenvman.2025.124066). In the second chapter, I investigated how fires impact the taxonomic and functional diversity of bird communities in the Atlantic Forest. For this, we sampled bird communities in the Cantareira-Mantiqueira Ecological Corridor in São Paulo State. My goal was to assess whether there are differences in bird species composition between burned and unburned forests. Additionally, I evaluated whether diversity indices respond to variables such as forest cover, primary productivity, fire size, and fire severity. This chapter is titled 'Fire size and vegetation productivity shape bird diversity across burned landscapes in the Brazilian Atlantic Forest' and was submitted to the Journal of Applied Ecology.

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Chapter I: Relative fire-proneness of land cover types in the Brazilian Atlantic Forest

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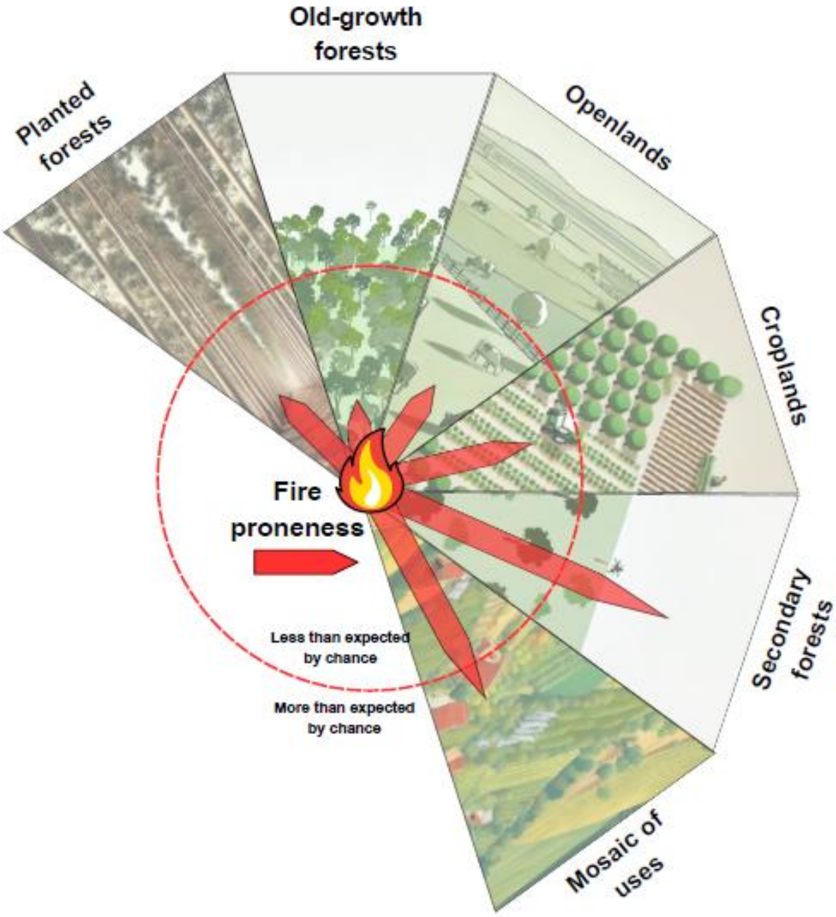
Graphical abstract



Abstract

Fires are increasingly affecting tropical biomes, where landscape-fire interactions remain understudied. We investigate the fire-proneness—the likelihood of a land use or land cover (LULC) type burning more or less than expected based on availability—in the Brazilian Atlantic Forest (AF). This biodiversity hotspot is increasingly affected by fires due to human activities and climate change. Using a selection ratio-based approach, we analyzed fire-LULC interactions in 40,869 fires over a 35-year period (1987-2022) across various ecoregions in the AF. Our findings revealed that secondary forests, forest areas that have regrown after major disturbances, burned 61% more than expected by chance, whereas old-growth forests, native forests that have developed over very long periods, burned 57% less than expected, highlighting a nearly inverse relationship in their fire-proneness. Interestingly, our data indicate that pastures in the AF are less prone to fire than expected, despite being considered among the land uses that burn the most in Brazil. Other LULCs showed variable fire-proneness, with some differences between ecoregions. Over time, the fire-proneness of secondary forests decreased, likely due to forest aging and changes in land management practices. We emphasize the necessity for tailored fire management strategies that address the unique vulnerabilities of secondary forests, particularly in the context of ongoing restoration efforts aimed at increasing native forests. Effective measures, including the implementation of 'fire-smart management' practices and enhancing the perceived value of secondary forests among local communities, are crucial for mitigating fire risks. Integrating these strategies with incentive-based approaches can bolster fire prevention, ensuring the long-term success of restoration programs. Our study provides a framework for understanding fire-landscape dynamics in tropical forests and offers actionable insights for practitioners working to safeguard these biomes from the escalating threat of wildfires.

KEYWORDS: Wildfire; Fire-proneness; Land cover; Secondary forests; Old-growth forests; Fire management; Atlantic Forest

Introduction

Tropical forests are fire-sensitive biomes, with species lacking evolutionary adaptations to frequent fires and other aspects of fire regimes (Hoffmann et al., 2012; Pivello et al., 2021). Historically, these biomes experienced fires every few hundred years (Bush et al., 2008), but climate change and human activities have altered the frequency and nature of these events (Cochrane, 2003; Fonseca et al., 2019; Le Page et al., 2017). Fires now occur every decade or even annually, often escalating in size and severity (Cochrane, 2003; Flannigan et al., 2009; Uhl & Kauffman, 1990). Fires in tropical forests typically occur as low-severity surface fires, which consume the dry litter layer and result in the death of small trees and seedlings (Barlow et al., 2002; Staver et al., 2020; Uhl & Kauffman, 1990). These surface fires can escalate to high-severity fires, killing most large trees with thin bark. The resulting canopy openings increase sunlight penetration, which dries out the forest and creates conditions favorable to subsequent fires (Sansevero et al., 2020; Pivello et al., 2021). Hence, fires are associated with biodiversity changes (Kelly et al., 2017; Kelly et al, 2020), soil degradation (Nadporozhskaya et al., 2018), erosion (Girona-García et al., 2024), impacts on freshwater ecosystems (Vaz et al., 2014, 2021), diminished water retention (Sansevero et al., 2017; Schmerbeck & Fiener, 2015), and landscape dynamics alterations (Silva et al., 2011; Moreira et al., 2011).

Fires are particularly worrying in the Atlantic Forest (AF) biome, one of the world's most important biodiversity hotspots, which has high endemism (Myers et al., 2000). Originally, the AF covered 160 million hectares across coastal and inland portions of Brazil, Argentina, and Paraguay (Muylaert et al., 2018). This biome is the most degraded and deforested Brazilian biome, having suffered from intense land use and land cover (LULC) changes in recent centuries (Rezende et al., 2018). Most old-growth forests—native forests that have developed over long periods without significant disturbance—

were cleared to make way for human activities. Today, the AF retains only about 36% of its extent of natural vegetation. Most of this vegetation is highly fragmented, with 97% of forest patches being under 50 ha, isolated, and impacted by various human-induced disturbances (Ribeiro et al., 2009; Vancine et al., 2024). Despite these challenges, recent decades have seen improvements in vegetation cover due to conservation efforts led by the government and environmental organizations, aimed at reducing deforestation rates (Piffer et al., 2022). Also, the abandonment of agriculture and the depopulation of rural areas contributed to the resurgence of natural vegetation, particularly in the form of secondary forests—areas of forest that have regrown after major disturbances such as deforestation and fires, whose ecological value and recovery potential depend on the time since disturbance and the surrounding landscape context (Rezende et al., 2018; Souza et al., 2020; Vancine et al., 2024). Changes in Brazilian legislation, such as the Atlantic Forest Law in 2006 and the Brazilian Forest Code in 2012, are also expected to influence the fire-landscape dynamic over the years. However, despite strict regulations, fire is increasingly shaping the AF landscape (dos Santos et al., 2019), namely by resetting the gradual transitions from secondary forests to vegetation resembling old-growth forests. Fires disrupt regeneration processes and can shift the biome towards a savanna-like state (dos Santos et al., 2019; Sansevero et al., 2020).

Fires do not occur randomly across the LULC types of a given landscape; instead, their occurrence and spread are determined by a complex interplay of human actions and natural phenomena (Brando et al., 2016; Fonseca et al., 2019; Le Page et al., 2017; Pivello, 2011). In tropical forests, most fires are caused by humans as a result of using fire to clear or expand agricultural areas (da Silva Junior et al., 2020; Gois et al., 2020; Oliveira-Júnior et al., 2020). Fire spread through the landscape is influenced by wind, topography, vegetation structure, moisture content of the vegetation and soil, amount and composition of surface fuel load (Carmo et al., 2011; Moreira et al., 2009; Oliveira et al., 2014; Silva et al., 2009), and factors impacting firefighting efforts (de Assis Barros et al., 2022; Gutiérrez-Velez et al., 2014; Pivello et al., 2021). These factors interact with different LULC types, making some LULC types more susceptible to fire spread than others (Abreu et al., 2022; Fonseca et al., 2019; Gutiérrez-Vélez et al., 2014). We refer to this susceptibility as fire-proneness, reflecting the likelihood of a LULC type burning more or less frequently than expected based on its availability in the landscape. LULCs that are more fire-prone are likely to be disproportionately affected, beyond what would be expected by chance alone (Moreira et al., 2001).

In Brazilian tropical forests, fires disproportionately affect LULC types, with pastures and croplands being the most likely to burn (Abreu et al., 2022; Cano-Crespo et al., 2015; de Assis Barros et al., 2022; de Santana et al., 2020; Freitas et al., 2020; Gutiérrez-Vélez et al., 2014; Herrmann et al., 2023; Uriarte et al., 2016). Conversely, a negative correlation is expected between fire occurrence and spread and the cover of old-growth forests (de Assis Barros et al., 2022; Fonseca et al., 2019; Singh & Huang, 2022). This low fire-proneness among old-growth forests can be attributed to their remarkable retention of transpired moisture, which effectively reduces susceptibility to fire (Cochrane et al., 1999; Uhl et al., 1988). Unfortunately, ongoing transitions from old-growth forests to other types of LULC can often result in increased fire-proneness (de Assis Barros et al., 2022; Eva & Lambin, 2000; Fonseca et al., 2019; Singh & Huang, 2022). Particularly, changes from old-growth forests to secondary forests likely increase fire-proneness, as secondary forests are more vulnerable due to their differing species composition, lower moisture content, and elevated radiation and temperature conditions (Parsons et al., 2015; Fonseca et al., 2019; Gutiérrez-Vélez et al., 2014). Secondary forests in the AF typically emerge in degraded, abandoned pasturelands unsuitable for agriculture and livestock, and may also regenerate on the edges of small forest fragments, thus increasing the risk of fire (Guedes et al., 2020). As secondary forests mature and develop characteristics typical of old-growth forests, their fire-proneness is expected to decrease (Lebrija-Trejos et al., 2011; Ray et al., 2010).

Despite the extensive research on landscape-wildfire dynamics, critical gaps remain in our understanding of how fire-proneness varies among different LULC within Tropical Forests. In Brazil, the bulk of fire research has been conducted in the Amazon Forest, leading to a disproportionate focus that overlooks the distinct dynamics within the AF (dos Santos et al., 2019; Sansevero et al., 2020). Furthermore, no previous studies have comprehensively assessed the fire-proneness of different LULCs in Brazilian Tropical forests (see Carmo et al., 2011; Moreira et al., 2009; Oliveira et al., 2014). Instead, research has typically focused on examining the distribution of burned areas and the number of fire foci (Abreu et al., 2022; de Assis Barros et al., 2022; Gutiérrez-Vélez et al., 2014). Moreover, existing studies often overlook the heterogeneity of ecoregions in the AF, their cultural and socio-economic differences, as well as the interannual variability and drivers of fire activity, which likely impact fire dynamics. The ecoregions, including evergreen (ombrophilous) and seasonal forests, as well as transitional ecotone areas, are shaped by distinct temperature and rainfall patterns (Joly et al., 2014). Their distribution and fire proneness are also influenced by the AF's extensive longitudinal, latitudinal, and altitudinal variations (Marques et al., 2021). A lack of long-term studies further limits understanding of fire-LULC dynamics over time.

In this study, we used a selection ratio-based approach (e.g., Moreira et al., 2009) to analyze relative fire-LULC interactions across the ecoregions of the AF, examining data at five-year intervals over a 35-year period. By applying this established approach to tropical biomes, our study offers a novel assessment of fire-landscape relationships in this distinct region. We tested the following hypotheses. 1) Old-growth forests have low fire-proneness, irrespective of ecoregion or year analyzed. 2) Secondary forests exhibit high fire-proneness in all ecoregions compared to old-growth forests. 3) Secondary forests exhibit a decreasing trend in fire-proneness over the years as the average age of their patches increases and forests mature, resulting in more canopy closure and greater surface moisture. 4) Croplands, pastures, and other human-impacted LULCs exhibit variable fire-proneness dependent on ecoregion and year

Methods

We employed geospatial analyses to examine relative fire-proneness in different LULC types across the Brazilian AF ecoregions. Our workflow involved defining the ecoregions, obtaining and processing LULC and fire data, and estimating selection ratios to assess fire-proneness in each region.

Ecoregions

To assess how ecoregions affect fire-LULC interactions in the Brazilian AF, we analyzed the five regions that cover over 90% of the biome and record the most fires (Fig. 1). These ecoregions are defined by floristic compositions of typical genera and characteristic biological forms that recur within the same climate, potentially occurring on terrains with varied lithology but well-defined relief (IBGE, 2012). We utilized vector files from the Database of Environmental Information (IBGE; https://bdiaweb.ibge.gov.br), which employs the Brazilian Vegetation Classification to map and hierarchically organize the land cover across regions. The mapping methods are detailed in the IBGE's Technical Manual of Brazilian Vegetation (IBGE, 2012). The ecoregions are described as follows:

1) Semideciduous seasonal forest (SSF): Covering 37% of the biome, this largest

ecoregion in the AF is marked by two distinct seasons—rainy summers and dry winters. During the dry season, up to 50% of tree species undergo leaf shedding.

2) Decidual seasonal forest (DSF): Occupying 6% of the AF, these forests prevail at higher altitudes where temperatures are lower. Like the SSF, they experience two distinct seasons—rainy summers and dry winters. Over 50% of their tree species shed leaves during the dry season.

3) Dense ombrophilous forest (DOF): This region occupies 17% of the AF, forming a verdant belt along the Brazilian coast. Characterized by the absence of a dry season, it experiences consistently high precipitation year-round and maintains temperatures averaging above 25°C.

4) Mixed ombrophilous forest (MOF): Commonly known as 'Araucaria forests', these forests are notable for consistent high precipitation and a diverse mix of evergreen and deciduous species. Covering 15% of the AF, they are distinguished by a high prevalence of gymnosperm species, notably *Araucaria angustifolia*.

5) Contact areas (CA): Covering 15% of the AF, these undifferentiated plant communities represent transitional ecotone areas, which occur at the boundaries or within the interiors of different ecoregions. In the AF, these ecotones can be found between forests and open physiognomies, such as those typical of the Cerrado, as well as between different forest types, like evergreen and seasonal forests. These areas are often characterized by a mix of vegetation types with varying degrees of canopy closure, reflecting the transitional nature of the environmental gradients they occupy.

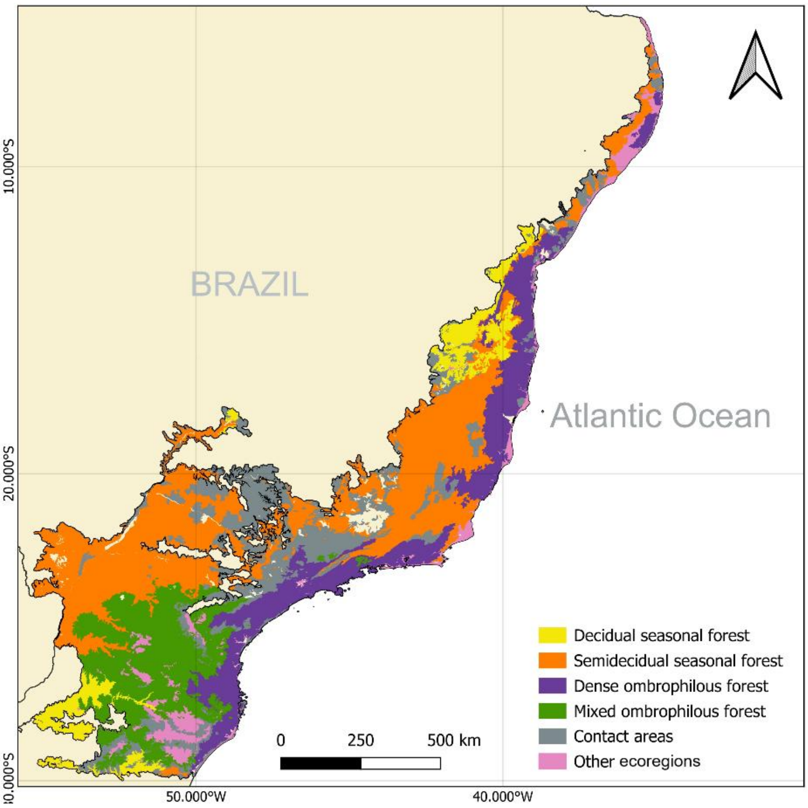


Figure 1. Study area. Ecoregions within the Brazilian Atlantic Forest.

Land cover maps

To obtain maps of LULC types in the ecoregions of the AF, we used maps from the MapBiomas platform - Collection 8.0 (available at https://brasil.mapbiomas.org). The MapBiomas Project is a collaborative Brazilian initiative that maps LULCs across the entire territory of Brazil. It uses satellite images, specifically from the Landsat program with a 30-m resolution, along with machine learning tools to create an annual time series of maps from 1985 to the present (Alencar et al., 2022). Transitions between classes are defined based on detectable changes in LULC, such as shifts from anthropogenic to forest classes, identified through algorithms that analyze satellite imagery. The platform also captures reversals, such as deforestation events, and secondary vegetation, where secondary vegetation is converted back to anthropogenic use. Additionally, the platform provides information on the age of secondary forests (da Silva Junior et al., 2020).

We selected eight LULC maps, one for each five-year interval, spanning from 1986 to 2021 (Vancine et al., 2024). This interval helps minimize temporal autocorrelation, enhancing the independence of subsequent assessments of fire-LULC interactions. This same interval was previously used to assess vegetation dynamics in the AF (Vancine et al., 2024). Next, we simplified the 30 LULC classes from MapBiomas Collection 8.0 into seven categories (Table 1), plus a 'Noncombustible areas' type, which was omitted from further analysis. This reclassification was based on vegetation structural similarities and potential for comparable fire behavior, particularly in terms of fuel structure and composition (Nunes et al., 2005).

Table 1. Characterization of land use and land cover types.

Land cover type	Definition	Land cover type in MapBiomas
Old-growth forests	Areas with native forest cover since the beginning of the historical MapBiomas series.	Forest Formation; Floodable Forest
Secondary forests	Areas that have transitioned from anthropogenic use to native forest vegetation. The transition period (vegetation age) can vary from 1 to 35 years.	The captions for secondary forest areas provide information about the age of the vegetation. In this context, we grouped all age ranges into a single category corresponding to secondary forests.
Openlands	Areas characterized by ground and shrub vegetation.	Savanna Formation; Herbaceous Sandbank Vegetation; Grassland; Pasture; Other Non-forest Formations
Temporary crops	Areas that are both sown and harvested within the same agricultural year, sometimes more than once.	Soybean; Sugar cane; Rice; Cotton; Other Temporary Crops
Perennial crops	Areas with plant species that are cultivated and live for more than two years without needing to be replanted annually	Coffee; Citrus; Palm Oil; Other Perennial Crops
Planted forests	Areas dedicated to silviculture, primarily consisting of *Eucalyptus* sp. and *Pinus* sp.	Forest Plantation

Mosaic of uses	Mix or combination of different land uses, creating a diverse and complex pattern across the landscape. It generally represents small areas that might include household agriculture and traditional cattle ranching (Almeida et al., 2016).	Mosaic of uses
Noncombustible areas	Areas with low vegetation density (fuel accumulation) or high humidity and water levels. This class was excluded from the analysis.	Mangrove; Hypersaline Tidal Flat; Wetland; Rocky Outcrop; Non vegetated area; Water

Fire data

To obtain maps of fires in the ecoregions of the AF, we used the MapBiomas platform – Fire Collection 2.0, which includes annual records of fire scars from 1985 to 2022 (MapBiomas, 2024). Similar to the LULC maps, this project also identifies burned areas through analyses of Landsat images with 30-m pixels, using the Normalized Burn Ratio (NBR) index (see more details in https://brasil.mapbiomas.org/metodo-mapbiomas-fogo/). To ensure greater accuracy in identifying the parts of the LULC that burned, we aligned our fire maps with our LULC data collection, which spans from 1986 to 2021 with a five-year interval, selecting fire maps from years that corresponded to one year after each LULC map. Consequently, our fire maps, also selected at five-year intervals, span from 1987 to 2022. The minimum fire extent was five hectares (see Pereira and Santos, 2003; Moreira et al., 2009; Silva et al., 2009; Carmo et al., 2011), with each fire assigned to an ecoregion of the AF.

Data analysis

To determine the relative fire-proneness of each LULC type, we employed a selection ratio-based approach. This method involved comparing, for each fire, the proportion of each LULC type within the burned area to its proportion in the total area (burned and unburned) available for burning. In our study, a landscape unit is therefore defined as the spatial mosaic of different LULC types within the total area available for burning.

To define the total area available for burning, several methods have been proposed in the literature. For example, Moreira et al. (2009) and Silva et al. (2009) defined circular buffers centered on each fire, with a radius corresponding to the size of the largest fire in the respective ecoregion, which was expected to approximate fire shapes in the absence of external influences. Alternatively, Oliveira et al. (2014) tailored buffers to the specific characteristics of each fire's perimeter, using a shape that mirrored the fire but was approximately twice its size. Our approach aligns with Oliveira et al. (2014) in creating buffers that mirror the shape of each fire, but we opted for a buffer size of approximately four times the fire area based on preliminary analyses indicating that a larger buffer was necessary in our study region to capture variations in LULC while minimizing overlap between fires. This method was originally proposed for the study of resource selection by animals (Manly et al., 1993) and has been applied in fire research studies (e.g., Moreira et al., 2009; Silva et al., 2009; Carmo et al., 2011; Oliveira et al., 2014).

The selection ratio (w_i) for a given LULC type *i* is an index estimated as $w_i = o_i/\pi_i$ (Manly et al., 1993), where o_i is the proportion of a burned patch belonging to LULC type *i* (estimated from the area consumed by fire) and π_i is the proportion of available area belonging to LULC type *i* (estimated from both the burned patch and the surrounding buffer). Selection ratios range from 0, if the LULC type is available but not consumed by the fire ($o_i = 0$), to a large value (in theory ∞), in the situation where the fire consumes the only tiny patch of a given LULC type that was available to burn (π_i approaches 0) (Moreira et al., 2009). To avoid these extreme *w* values in very small areas, we only analyzed LULC patches larger than 1 ha. If a given LULC type is burned in proportion to its availability, then *w*=1. If *w*>1, the LULC type is considered more fire-prone than expected by chance. Conversely, if *w*<1, the LULC type is considered less fire-prone than expected by chance. Since we were interested in the fire-proneness of LULC types per ecoregion, we omitted fires that, with their buffers, overlapped more than one region. A total of 40,869 burned patches were considered for analysis.

Next, we averaged values for each LULC type across the fires within a given ecoregion and estimated 95% confidence intervals. We considered differences between selection ratios for different classes significant when their respective confidence intervals did not overlap. Additionally, if the confidence interval of *w* did not include 1, we considered the class significantly more or less prone to fire than expected by chance.

Results

Of the 40,869 fires detected and analyzed between 1987 and 2022, 44% occurred in the SSF ecoregion, 21% in CA, and the lowest percentages were in MOF (9%) and DSF (7%) (Table 2). The mean fire size was 23 ha, ranging from 15 ha in MOF to 27 ha in SSF. Mosaic of uses, secondary forests, and old-growth forests, in that order, were the LULC types with the highest available areas across regions. The region with the highest proportion of old-growth forests coincides with the area with the most fires, the SSF. CA had the highest proportion of secondary forests.

Table 2. Number of fires (≥5 ha), mean fire size (ha), and percentage of area occupied by LULC type, all with 95% confidence intervals, by ecoregion.

			LULC types							
Ecoregion	No. of fires	Mean fire size (ha)	Old-growth forests	Openlands	Temporary crops	Perennial crops	Plantation forests	Mosaic of uses	Secondary forests	Noncombustible areas
Semideciduous seasonal forest	18287	20.88 ± 1.20	27.26 ± 0.04	11.04 ± 0.02	2.26 ± 0.02	1.37 ± 0.01	0.59 ± <0.01	33.34 ± 0.04	19.27 ± 0.04	4.88 ± 0.02
Decidual seasonal forest	2924	20.67 ± 1.50	18.80 ± 0.04	25.39 ± 0.06	0.02 ± <0.01	0.48 ± <0.01	0.86 ± 0.01	26.87 ± 0.06	26.25 ± 0.10	1.23 ± <0.01
Dense ombrophilous forest	7797	16.33 ± 0.70	22.76 ± 0.02	11.96 ± 0.02	2.39 ± 0.02	0.63 ± <0.01	1.46 ± 0.01	33.42 ± 0.06	21.20 ± 0.08	6.18 ± 0.02
Mixed ombrophilous forest	3472	13.91 ± 0.63	22.82 ± 0.06	9.97 ± 0.02	5.69 ± 0.02	0.62 ± <0.01	3.43 ± 0.03	29.03 ± 0.06	24.38 ± 0.10	4.07 ± 0.02
Contact areas	8389	16.79 ± 0.57	15.85 ± 0.02	13.76 ± 0.02	3.53 ± 0.02	1.51 ± 0.01	1.03 ± 0.01	21.14 ± 0.06	38.53 ± 0.12	4.65 ± 0.02

Fire-proneness across ecoregions

Across the ecoregions of the Brazilian AF, secondary forests were the most fire-prone type of LULC, while old-growth forests were the least fire-prone (Fig. 2). Secondary forests burned 61% more than expected by chance ($w = 1.61$), whereas old-growth forests burned 57% less ($w = 0.43$). Besides secondary forests, only the mosaic of uses LULC type was significantly prone to fire, with a selection ratio 5% higher than expected. Like old-growth forests, the LULC types openlands, temporary crops, and planted forests were also significantly less prone to fire than expected, with selection ratios between 31% and 35% below expected. Perennial crops were the only type of LULC to burn according to availability across AF's ecoregions (confidence interval of w included 1).

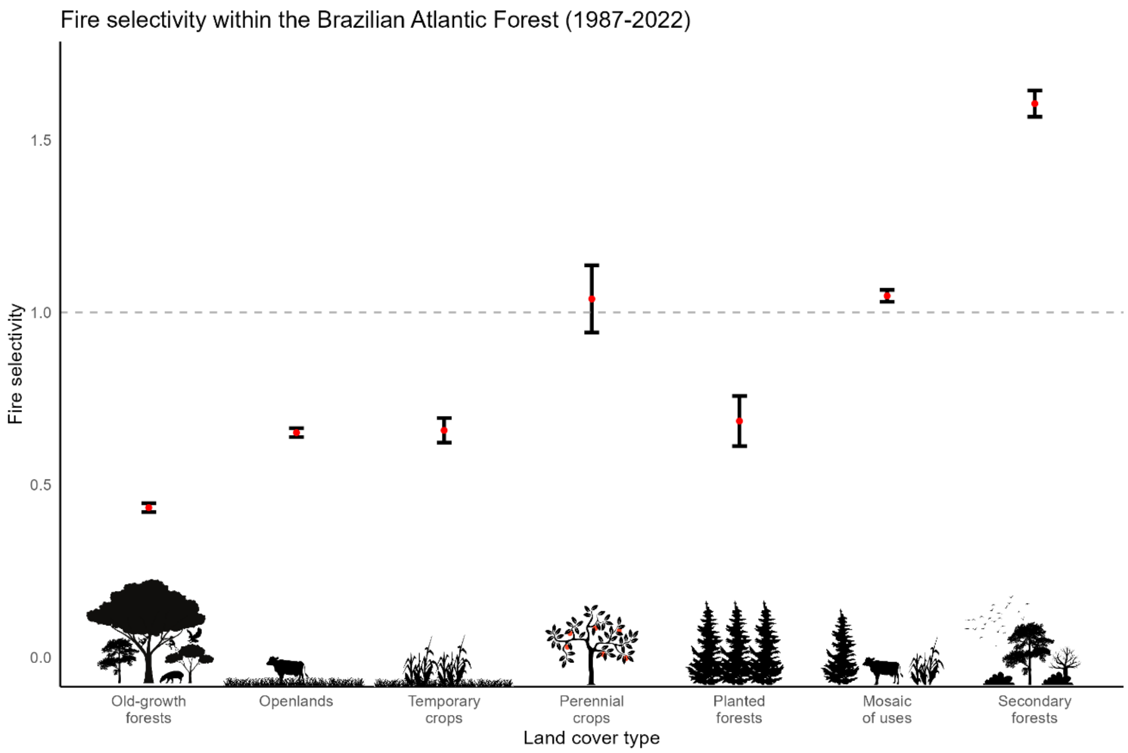


Figure 2. Mean selection ratios (w) with 95% confidence intervals for LULC types across ecoregions of the Brazilian Atlantic Forest. $w = 1$ indicates the LULC type burns according to availability; $w < 1$ means it burns significantly less, and $w > 1$ means it burns significantly more than expected by chance.

Fire-proneness by ecoregion

As hypothesized, old-growth forests had low fire proneness across ecoregions (Fig. 3), burning between 33% and 66% less than expected by chance, depending on the region. Except for the DSF region, this LULC type had the lowest selection ratio in all other regions. In contrast, with selection ratios between 46% and 87% above expected, secondary forests tended to have the highest fire proneness across regions, except for the DOF. Openlands had low fire-proneness, burning 20% to 59% less than expected, except in MOF where they burned according to availability. As expected, other human-impacted LULC types showed variable fire proneness, depending on the ecoregion.

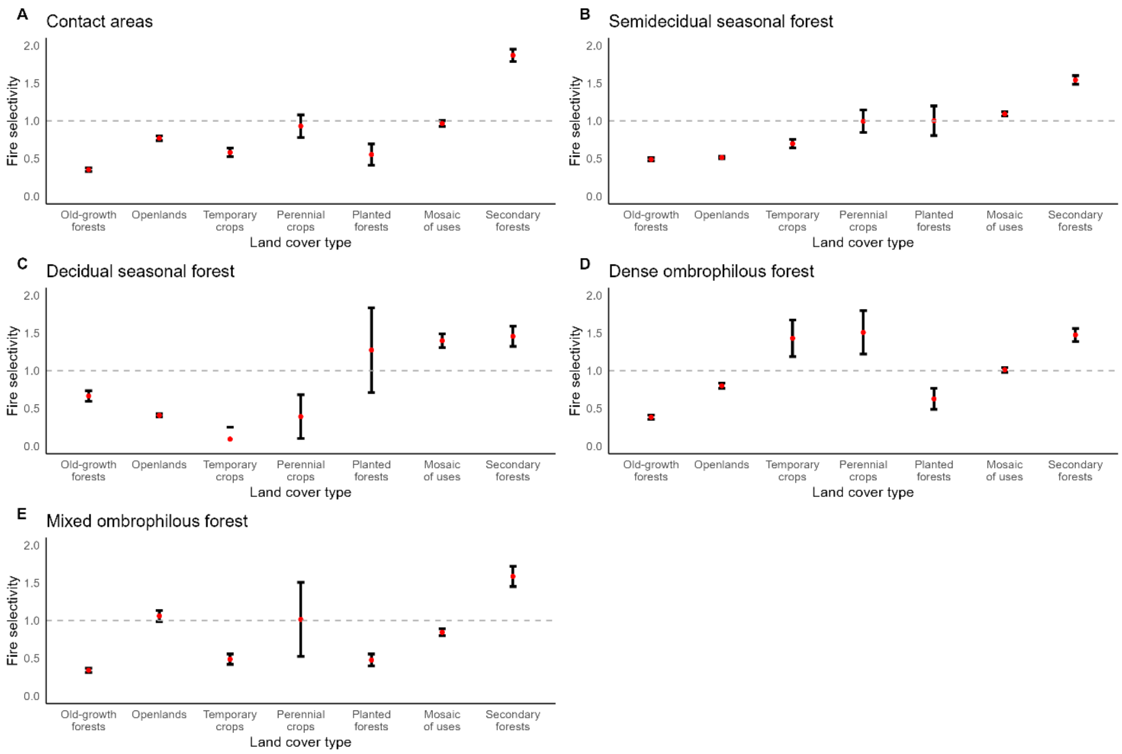


Figure 3. Mean selection ratios (w) with 95% confidence intervals for LULC types in each ecoregion of the Brazilian Atlantic Forest. Refer to Fig. 2 for more explanations.

Fire-proneness over time

The fire-proneness of old-growth forests remained consistently low over the 35-year study period (Fig. 4), showing no pattern of increase or decrease. Likewise, openlands and temporary crops generally had low fire-proneness, with no clear change over time, although temporary crops burned according to availability in 1992. Perennial crops, which generally burned in proportion to availability until 2012, became less prone to burning than expected from that year onwards. Forest plantations consistently had low fire-proneness, except in 1992 and 2002 when their fire-proneness was neutral. Mosaic of uses showed mixed fire-proneness over the years but shifted to a significantly lower than expected fire-proneness from 2012 onwards. It burned in proportion to its availability in 1992 and 2012, had high fire-proneness in 1987 and 1997–2007, but had low fire-proneness in 2017 and 2022. Secondary forests followed the hypothesized trend of decreasing fire-proneness, being significantly prone to fire until 2012, then burning in proportion to their availability from that year onwards.

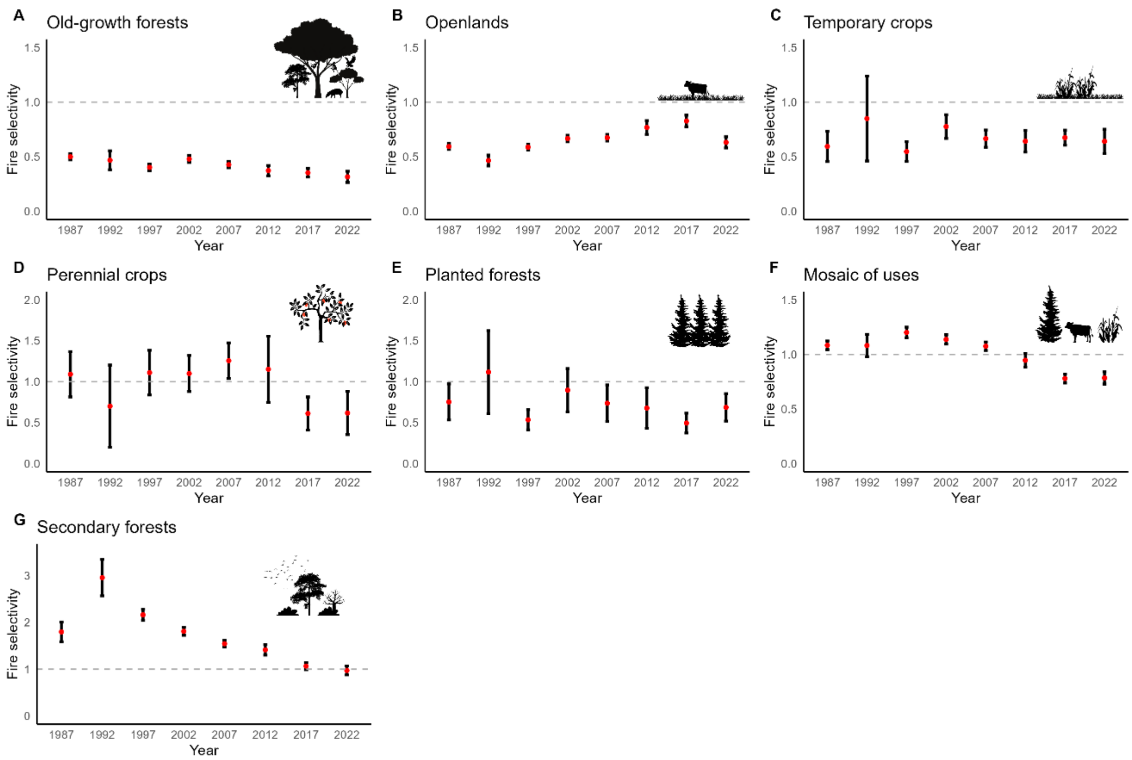


Figure 4. Mean selection ratios (*w*) with 95% confidence intervals for LULC types across ecoregion of the Brazilian Atlantic Forest from 1987 to 2022. Refer to Fig. 2 for more explanations.

Discussion

Our analysis spanning over 35 years of fire-LULC interactions in the Brazilian AF ecoregions provides insight into the relative fire-proneness of different LULCs in a tropical biome. This is critical as fire becomes a growing issue both worldwide and in these biomes. Across all ecoregions, our results confirmed the low fire-proneness of old-growth tropical forests, in contrast with the high fire-proneness of secondary forests. Other LULCs showed more variable fire-proneness, with some differences between ecoregions. Furthermore, fire-proneness has changed over time in several LULCs, suggesting that these trends may be driven by natural ecological succession, climatic conditions, or human actions potentially influenced by changes in Brazilian environmental legislation. Notably, we found a decline in the fire-proneness of secondary forests over time, likely due to their lower susceptibility as the average age of these patches in the landscape increases, resulting in characteristics increasingly similar to old-growth forests.

Fire-proneness in the Brazilian Atlantic Forest

By confirming the low fire-proneness of old-growth tropical forests, our results are consistent with studies indicating a reduced risk and density of fires in undisturbed forests within the AF (de Assis Barros et al., 2022; Guedes et al., 2020; Singh & Huang, 2022). Despite the significant fragmentation and deforestation in the AF (Ribeiro et al., 2009; Vancine et al., 2024), we demonstrated that, in general, old-growth forest fragments still remain the LULC type least likely to burn compared to all others. The low fire-proneness of tropical old-growth forests can be attributed to their retention of transpired moisture and the trees' substantial contribution to forest humidity, which limits fire ignition and spread (Cochrane, 2003; Cochrane et al., 1999). Interestingly, our data showed that the likelihood of old-growth forests burning less than expected across regions was similar to that of secondary forests burning more than expected, both at approximately 60%.

The high fire-proneness of secondary forests was anticipated, as they exhibit high fuel load, low moisture content, and high radiation and temperature in the understory (Gutiérrez-Vélez et al., 2014; Hasselquist et al., 2010; Kyereh et al., 2007). The flammability of secondary forests—associated with their different species composition—may be influenced by the functional traits of their species (e.g., leaf thickness and surface area), which can change throughout the successional process (Parsons et al., 2015). Moreover, the spatial arrangement of these areas likely influences the fire spread, as they may be closer to anthropized areas and sources of ignition. This result is also consistent with previous works in the Amazon Forest that found higher fire activity in degraded forests (Balch et al., 2015; Brando et al., 2014, 2016; Cochrane et al., 1999). Research further suggests that, because secondary forests are often viewed as having low economic value, farmers may be less motivated to prevent them from burning when nearby fires pose a threat (Sorrensen, 2000). Other studies also show a link between deforestation fires to expand agricultural areas and the high fire-proneness of secondary forests (Pivello et al., 2021). Despite Brazilian legislation prohibiting fires, except in specific situations, farmers still burn secondary forests in pastures and agricultural areas to prevent forest encroachment. Furthermore, these areas are often re-cleared within the first few years following forest establishment (Piffer et al., 2022).

Among the LULC types significantly less prone to fire, the results for openlands, where pastures are included, were noteworthy. Despite pastures having the largest burned areas in Brazil (Alencar et al., 2022; Moreira de Araújo et al., 2012) and being generally associated with fire risk (Guedes et al., 2020; Gutiérrez-Vélez et al., 2014; Herrmann et al., 2023), our findings indicate lower-than-expected fire proneness. This shows the advantage of our selection ratio-based approach, as this method allows a distinction to be made between when a LULC type burns extensively due to its abundance in the landscape and when it burns disproportionately more than its availability. On the contrary, previous works have generally highlighted the large representativeness of pastures within the burned areas, overlooking the total available area that could have potentially burned in the landscape, which is usually also substantial. Indeed, although pastures occupy around 30% of the AF (Dos Santos et al., 2022; Souza et al., 2020), our results show that their fire proneness is likely lower than expected when availability per fire is taken into account. The high association of fire with pastures found in other studies may not be due to a positive selectivity compared to other land covers, but rather to the frequent illegal use of fire for cleaning and renewal pastures (Moreira de Araújo et al., 2012). It should be noted that although our results indicate lower fire proneness for pastures than expected by chance, pasture fires still pose a threat to the AF by contributing to the spread of fires to other fire-prone LULCs (Guedes et al., 2020).

Management-related aspects of the other LULC types that were significantly less prone to fire, such as temporary crops and planted forests, or that burned according to availability, like perennial crops, should be stressed. Managed croplands usually exhibit low fuel load and high moisture content due to irrigation (Duguy et al., 2007). Planted forests, on the other hand, are often intensively managed by private companies to avoid fire hazards (Guedes et al., 2020; Mirra et al., 2017). Additionally, these LULCs are typically closer to urban areas, roads, and scattered populations. This proximity may result in more frequent fire occurrences (dos Santos et al., 2019; Barros et al., 2022), but it also facilitates faster fire detection and easier firefighting efforts, reducing burned extent and fire proneness (Moreira et al., 2009).

Lastly, it was to be expected that mosaic of uses would be prone to fire across ecoregions. These areas typically consist of small properties where slash-and-burn practices are employed to renew the land and eliminate waste. Subsistence farmers and indigenous populations often use these fires, confining them to small areas with localized impacts (Pivello et al., 2021). However, there is a significant risk that these fires could accidentally spread to nearby fire-prone LULCs. Under climate change scenarios, the risk of fire increases, especially when traditional agricultural fire practices result in accidents or loss of control (Pivello et al., 2021). It is crucial to develop strategies that balance traditional practices with modern fire management to mitigate these risks effectively.

Fire-proneness by ecoregion

Although it was hypothesized and therefore unsurprising that the old-growth forests of the AF exhibit consistently low fire-proneness with minimal variation between ecoregions, it is nonetheless remarkable that this low fire-proneness remains uniform across regions characterized by dry seasons, such as SSF and DSF, as well as in regions with evergreen vegetation, like ODF. These results reinforce the reduced fire-proneness of tropical forests (Cochrane, 2003; Cochrane et al., 1999), even under disparate regional conditions. Yet, previous studies have also shown that altitude, mean annual temperature, and drought severity can be positively associated with fire occurrence and lead to variations in the area burned in the AF (Abreu et al., 2022; de Assis Barros et al., 2022; de Santana et al., 2020; Herrmann et al., 2023; Singh & Huang, 2022).

In the AF, regions with varying economic development can show different success rates in restoration programs (Piffer et al., 2022), affecting fire prevention and control. In the Brazilian Amazon, studies show that federal and state agencies, with distinct institutional capacities, implement diverse fire management practices, contributing to regional differences in fire management (Fonseca-Morello et al., 2017). In Portugal, research also shows that regions with different climatic and environmental conditions present LULCs with different fire-proneness (Moreira et al., 2009). In our study, this is likely why the LULC openlands type, which generally had low fire-proneness in most AF ecoregions, exhibited higher fire-proneness, burning according to its availability, in the MOF region. This result is likely influenced by both the environmental and cultural context of the MOF ecoregion. This ecoregion is characterized by higher average altitudes and lower temperatures (IBGE, 1992), and is primarily concentrated in southern Brazil. Unlike the southeastern and northeastern regions, where intensive agriculture predominates, southern Brazil has a larger number of properties engaged in family farming. In these settings, the use of fire in pastures is a traditional practice (Carvalho & Andrade-Filho, 2019). Additionally, some southern states, such as Rio Grande do Sul, grant municipalities the authority to authorize and supervise the use of fire in pastures (Law No. 13,931, 2012). These regional differences are likely related to the smaller average fire sizes observed in this ecoregion compared to others.

Despite the environmental, cultural, social, and economic differences between ecoregions, the secondary forest LULC type burned more than expected by chance in all AF regions, as predicted. Not even the consistently high rainfall in evergreen ecoregions such as ODF (Oliveira et al., 2000) reduces the fire-proneness of secondary forests, highlighting the vulnerability of this LULC to such disturbance. Still, our results show that secondary forests are almost twice as fire-prone in CA as in DSF, with selection ratios 87% and 46% higher than expected, respectively. This may be due to the fact that CAs are mainly transition zones between the AF biome and the Brazilian Cerrado. Unlike the AF, the Brazilian Cerrado is a fire-dependent system, with ecological communities adapted to this disturbance (Pivello et al., 2021). As such, the greater proximity of CA's secondary forests to the Cerrado is likely to explain their greater fire proneness. Likewise, as in the Cerrado, where cattle ranching is the leading cause of fire (Pivello et al., 2011), secondary forests in the CA regions are also burned to expand pasturelands. Worryingly, fires in secondary forests can promote the growth of herbaceous species and lead to the replacement of forests by non-woody vegetation types. This shift is concerning, as positive feedback loops with fire can maintain these new vegetation types, which is a growing issue in tropical forests worldwide (Pivello & Coutinho, 1996; Sansevero et al., 2020).

Fire-proneness of the Brazilian Atlantic Forest over time

Our results also confirmed the hypothesis that AF old-growth forests would exhibit consistently low fire-proneness over time, with minimal variation across the sampling years. Not even the inclusion of a major El Niño year (1996–1997) among the years sampled altered this consistency, despite major El Niño years being associated with extreme droughts and a greater potential for fires to occur and spread (Aragão et al., 2018; Marengo et al., 2018). In fact, this El Niño event does not seem to have altered the fire-proneness in 1997 or the chronosequential fire-proneness pattern for any LULC type studied. However, the years sampled did not include other extreme climatic events, such as the major La Niña (characterized by high precipitation) in 1988–1989 or the major El Niño in 2015-2016. Therefore, it remains possible that some LULC types had unusual fire-proneness patterns during these events. Future studies on fire-landscape interactions in the AF should include specific climatic drivers, such as variations in precipitation, temperature anomalies, and the occurrence of extreme weather events associated with major El Niño and La Niña phenomena.

The hypothesized decreasing fire-proneness trend of secondary forests over time was confirmed and the result can be discussed in light of two main reasons. First, the early data from the MapBiomas collection that we used to obtain the LULC maps only included young secondary forests. Over time, the collection encompassed a broader range of ages for this LULC type, leading to an increase in the average age of secondary forest patches included in the annual maps. Thus, the reduced fire-proneness of secondary forests in more recent years, burning in proportion to availability from 2012 onwards, is likely partly due to the increased age of these forests. Forest succession leads to significant environmental changes, with early stages having higher temperatures and lower humidity in the understory, transitioning to cooler and more humid conditions in later stages (Ray et al., 2010; Lebrija-Trejos et al., 2011). However, the approximate maximum age of the secondary forest patches in our data in 2022, 35 years, combined with the existence of younger patches, means that this LULC type has not yet reached the tipping point of having characteristics close enough to old-growth forests to become equally less prone to fire. Future studies must analyze the age of each patch of secondary forest so that we can understand more precisely after how long this type of LULC becomes less prone to fire than expected by chance.

The second reason for the decreasing fire-proneness is that early-stage secondary forests are often burned to prevent encroachment on agricultural areas. In the AF, regenerated forests in pastures and areas of shifting cultivation—where land is alternately farmed and left to regenerate—are frequently re-cleared before reaching advanced succession stages (Piffer et al., 2022), thus avoiding stricter protection under the Atlantic Forest Law (Law No. 11.428/2006). This law strictly regulates the cutting of native vegetation, allowing it in initial, medium, and, under exceptional circumstances, advanced regeneration stages, provided appropriate authorization is obtained and sustainable management criteria are met. On the other hand, legislation changes may also be behind the shift to low fire-proneness from 2012 onwards for the perennial crops and mosaic of uses LULC types, after the approval of the New Brazilian Forest Code (Law nº 12.651/2012). Firefighting may well have become more effective in these LULCs after the enactment of this law, which devotes a chapter to the prohibition and control of wildfires.

Management implications

Our results show that secondary forests have disproportionately burned the most across all regions of the AF in the past few decades, emphasizing the need for fire management strategies to carefully address this LULC. This is even more crucial considering that numerous restoration programs have restored millions of hectares of native vegetation, primarily as secondary forests, in recent decades (dos Santos et al., 2019; Brancalion et al., 2019; Vancine et al., 2024). It is clear that a trade-off must be established between the benefits of increasing secondary forest areas and the costs of protecting them, especially in the early years, to avoid a greater risk of fire in the landscape. Fire will lead to the interruption of forest succession to mature forests (Cochrane, 2001; Cochrane et al., 1999; Sansevero et al., 2020). Implementing effective fire prevention and management measures in secondary forests will be necessary to safeguard the restoration efforts and ensure their long-term success (dos Santos et al., 2019). Some authors simply argue that in the face of deforestation fires, which are illegal but still used in secondary forests, law enforcement should be the primary response, defending that fines should then be used to fund law enforcement (Pivello et al., 2021).

By showing such a large discrepancy in fire-proneness between secondary forests and other LULC types, our data also suggest incorporating integrated landscape approaches from fire-prone landscapes in Mediterranean regions and North America (Pivello et al., 2021). One such approach is 'fire-smart management', which involves managing the entire landscape to reduce fire risk. In this context, implementing low fire risk matrices composed of LULC types that our results have shown to be less prone to fire around secondary forests can be an effective strategy to prevent the spread of fire. For example, there is evidence that eucalyptus plantations provide some protection against fire, because plantation owners seek to suppress and control fires that could otherwise harm their eucalyptus investments (Guedes et al., 2020). Using this type of LULC around more fire-prone patches, including mosaic of uses, may be an option to consider. Other approaches could involve forest management strategies, such as controlling exotic grasses to reduce fuel loads and mitigate severe fire risks. Dedicated teams exclusively focused on these efforts are essential (North et al., 2021).

The fire-proneness of secondary forests in the AF also highlights the need to increase their perceived value by local communities to prevent them from burning (Guedes et al., 2020). This could involve enriching younger forest patches (e.g., up to 5 years old) with fruit or timber trees and offering payments for ecosystem services such as carbon sequestration, water regulation, and habitat restoration (Guedes et al., 2020). Some authors suggest that financial institutions could offer better loan conditions and payment rates to farmers with a good fire governance record (Nepstad et al., 2014). Similarly, commodity buyers may provide favorable terms to farmers that adhere to the rules (Pivello et al., 2021). Lastly, the AF should contain programs dedicated to forecasting and monitoring wildfires, like those in the Amazon Forest. In this scenario, plans to combat and prevent fires should be developed well in advance, taking into account alerts for areas with high deforestation rates, especially those with secondary forests (Pivello et al., 2021).

A few regional differences across ecoregions in fire-proneness underscore the importance of tailored fire management strategies, which could be evaluated and refined through future implementation. These methods can be adapted to the specific socioeconomic and environmental contexts of each region. In the MOF, where family farming and traditional burning practices are common (Herrmann et al., 2023), stricter regulations and monitoring could help address the greater fire-proneness of openlands. Conversely, in the DOF—the only ecoregion where croplands (both perennial and annual) were more fire-prone than expected—strategies should focus on reducing fire spread and severity in these agricultural areas. Such approaches, including the removal of exotic grasses and thinning efforts, have already been proposed for fire-dependent ecosystems to mitigate fire risk and enhance ecological stability (North et al., 2021). In the CA ecoregion, buffer zones with managed vegetation could reduce fire spread in transition areas to the Cerrado biome, addressing the higher susceptibility of secondary forests in this region. These ecoregion-specific insights lay the groundwork for future research to test and refine tailored fire management strategies.

Conclusion

This study used a selection ratio-based approach in 40,869 fires spanning over 35 years to evaluate the relative fire-proneness of LULC types in a tropical biome for the first time. This method compares, per fire, the proportion of each burned land cover type with its availability nearby. Our findings quantified the variation in fire-proneness across LULC types within the Brazilian AF, highlighting that the likelihood of secondary forests burning more than expected was approximately 60%, mirroring the 60% likelihood of old-growth forests burning less than expected. Interestingly, pastures, included in openlands, exhibited lower-than-expected fire proneness despite their large burned areas in Brazil. Secondary forests burned more than expected in all AF regions, with a particularly high fire-proneness in CA, transition zones between the AF and the Cerrado, a fire-dependent system. The observed trend of decreasing fire-proneness in secondary forests over time likely reflects both the increasing age and maturity of these forests and changes in land management practices.

We emphasize the necessity for tailored fire management strategies that address the unique vulnerabilities of secondary forests, particularly in the context of ongoing restoration efforts aimed at increasing forest cover. Effective measures, including the implementation of 'fire-smart management' practices and enhancing the perceived value of secondary forests among local communities, are crucial for mitigating fire risks. Integrating these strategies with robust law enforcement and incentive-based approaches can bolster fire prevention and control, ensuring the long-term success of restoration programs. Our analysis provides a framework for understanding fire-landscape dynamics in tropical forests and offers actionable insights for policymakers, conservationists, and land managers working to safeguard these biomes from the escalating threat of wildfires.

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Chapter II: Fire size and vegetation productivity shape bird diversity across burned landscapes in the Brazilian Atlantic Forest

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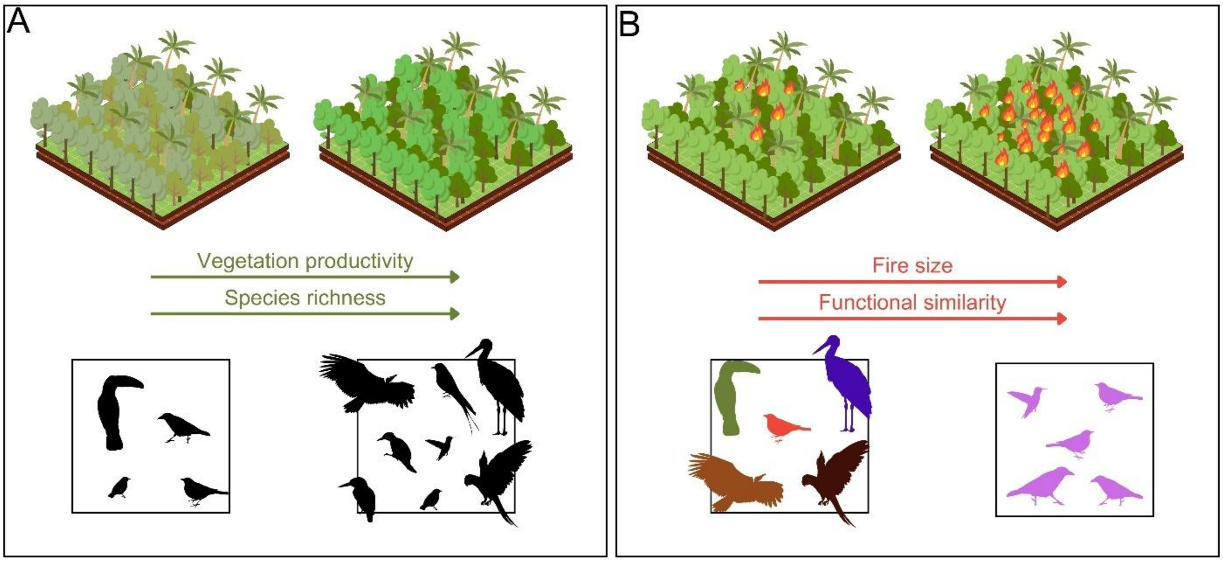
Graphical abstract



Abstract

1. Fires pose an increasing threat to tropical forests worldwide. However, few studies have attempted to evaluate their impacts on bird communities. Consequently, the responses of tropical birds to this disturbance remain unclear.
2. We assessed bird community composition, species richness, and functional diversity between unburned and burned forests across 15 landscapes in the Brazilian Atlantic Forest. Additionally, we analyzed how these indices were influenced by native forest cover, vegetation productivity, fire severity, and fire size. To address these questions, we applied generalized linear mixed models.
3. Unburned and burned forests consistently exhibited similar bird species composition, species richness, and functional diversity. Species richness was positively associated with vegetation productivity. Functional diversity was primarily explained by fire size, with the magnitude and direction of the effects varying according to the functional index used and the forest type.
4. Functional divergence showed a positive correlation with fire size in unburned forests and a negative correlation in burned forests. Functional dispersion, when considering communities across both forest types, was negatively correlated with fire size.
5. *Synthesis and applications*: This study highlights how bird communities in the Brazilian Atlantic Forest respond to fires. Our findings suggest that fires alone do not significantly alter bird community composition and diversity. However, bird responses are influenced by vegetation productivity and fire size. We emphasize the need for tailored fire management strategies aimed at reducing forest degradation and fire occurrence. Effective measures, such as forest restoration and the implementation of 'fire-smart management' practices, are essential to safeguard bird diversity. These results underscore the need for proactive governmental policies to prevent and manage fires in the Atlantic Forest, particularly in highly degraded landscapes.

Keywords

avian ecology, fire ecology, fire management, landscape ecology, landscape management, tropical fires, wildfire

Introduction

Historically, tropical forests experienced only occasional fires, with intervals spanning hundreds of years, typically associated with extreme drought conditions (Uhl & Kauffman, 1990). However, due to the combined impacts of human activities and climate change, fire frequency has increased, and return intervals have shortened to decades or even less (Le Page et al., 2017). Unlike fire-dependent biomes (e.g., savannas), tropical forests are highly sensitive to fire because their species lack evolutionary adaptations to withstand such disturbances (Pivello et al., 2021). In tropical forests, fires generally occur as low-intensity surface fires that burn through the dry litter layer, leading to the death of smaller trees and seedlings (Uhl & Kauffman, 1990; Barlow et al., 2002; Staver et al., 2020). Under extreme drought conditions, these surface fires can intensify into high-severity fires that may kill larger, thin-barked trees (Uhl & Kauffman, 1990). Consequently, fires are associated with shifts in biodiversity, soil degradation, increased erosion, reduced water retention, impacts on freshwater ecosystems, and alterations in landscape dynamics (Carmo et al., 2011; Sansevero et al., 2020; Schmerbeck & Fiener, 2015; Vaz et al., 2014).

Birds are primarily affected by fires due to changes in vegetation, although they may also experience direct impacts from smoke and flames (Mardiastuti, 2020). While such impacts generally do not alter species richness within communities, they can lead to shifts in species composition, often replacing highly specialized and rare species with those better adapted to disturbed habitats (Barlow et al., 2002; Mestre et al., 2013). Fire-related studies on bird communities typically focus on local environmental variables, such as canopy openness and understory vegetation, often overlooking broader landscape-scale features. For instance, the amount of native forest cover may play a crucial role in influencing bird communities during and after fires, acting as ecological refuges and sources for recolonization (Robinson et al., 2014; Watson et al., 2012). Vegetation productivity, in contrast, can be used as a proxy for resource availability and determine bird occurrence within burned landscapes (Pettorelli et al., 2005; Leveau & Isla, 2021). Moreover, fire characteristics—such as fire size and fire severity—are strongly associated with changes in resource availability, which can disrupt post-fire occupancy patterns and landscape connectivity (Parkins et al., 2018; Steel et al., 2018, 2022).

Fire impacts on bird communities are often assessed using species richness or by comparing species composition between unburned and burned forests, with less emphasis on functional diversity (Hidasi-Neto et al., 2012; Sitters et al., 2016). Functional diversity indices, however, go a step further by incorporating species' ecological roles, allowing measurement of the range, abundance, and distribution of functional traits within communities. This approach creates a direct link between species diversity and ecosystem functioning (Tilman et al., 1997). Understanding fire impacts on functional diversity is therefore essential, as it can be associated with ecosystem resilience (Walker, 1995).

In Brazil, fire-related studies in tropical forests are concentrated within the Amazon biome, with significantly less emphasis on the Atlantic Forest biome. As one of the world’s critical biodiversity hotspots, the Atlantic Forest has experienced intense deforestation and land-use changes over recent centuries, resulting in a highly fragmented and degraded forest mosaic (Rezende et al., 2018; Ribeiro et al., 2009). This fragmentation exacerbates fire risks, as fragmented patches with exposed, dry edges become increasingly prone to ignition, particularly in areas near human-altered landscapes (Cochrane et al., 1999). The interaction between fire and fragmentation creates a reinforcing feedback loop: recurrent fires exacerbate the degradation of forest fragments, delaying or even preventing regeneration while fostering conditions that promote further fire events (Cochrane et al., 1999; dos Santos et al., 2019; Driscoll et al., 2021; Sansevero et al., 2020). Over time, this feedback loop can lead to large-scale ecological shifts, transforming forests into non-forest ecosystems and compromising the biome's unique biodiversity and resilience (dos Santos et al., 2019; Sansevero et al., 2020). Given the increasing fire threat to the Atlantic Forest, understanding its impacts on biodiversity is crucial for developing and implementing effective conservation strategies.

In this study, we examined the relationship between fire and bird diversity – measured as species richness and functional indices – in the Atlantic Forest. We focused on differences in diversity and community composition between unburned and burned forests. Additionally, we analyzed how bird diversity is influenced by landscape features such as forest cover, vegetation productivity, fire severity, and fire size. To address these questions, we proposed the following hypotheses:

Bird communities are expected to exhibit a diversity pattern similar to that observed in Amazonian communities (Barlow et al., 2012; Mestre et al., 2013), with no significant differences in overall diversity between unburned and burned forests. However, species composition is anticipated to differ between these environments, as forest-dependent and disturbance-sensitive species are likely to be replaced by more generalist species adapted to degraded habitats (Barlow et al., 2002; Morante-Filho et al., 2015).

Bird diversity is expected to be positively correlated with the extent of native forest cover and vegetation productivity. Larger forest fragments and environments with greater net primary productivity provide more resources, making them strong predictors of bird diversity (Pettorelli et al., 2005; Leveau & Isla, 2021; Watling et al., 2020). Conversely, bird diversity is anticipated to be negatively correlated with fire severity and fire size, as fires disrupt vegetation structure and landscape configuration, reducing habitat quality, connectivity, and resource availability (Parkins et al., 2018; Steel et al., 2018, 2022).

Methods

Study region

We conducted this study in the Cantareira-Mantiqueira Mountain corridor, located within the ombrophilous forests of the southeastern Brazilian Atlantic Forest, in the state of São Paulo (Fig. 1A). Originally spanning approximately 1.6 million km² (Muylaert et al., 2018), the Atlantic Forest has undergone substantial anthropogenic transformation, with a large portion of its area replaced by human land uses. Currently, approximately 36% of its natural vegetation remains (Vancine et al., 2024). Most of the surviving forest fragments are small, isolated, and subject to varying degrees of anthropogenic disturbance (Ribeiro et al., 2009; Vancine et al., 2024). In our study region, native vegetation predominantly comprises secondary forests that have regenerated following land abandonment (Rosa et al., 2021). The remaining old-growth forests are largely restricted to inaccessible areas with limited agricultural potential, often located on hillsides, steep slopes, or within protected areas, such as Cantareira, Juquery, and Jaraguá State Parks (Arzolla, 2002). Land use and land cover in the region are dominated by pastures and eucalyptus plantations, with few areas allocated to other human activities (Barros et al., 2019). The regional climate is classified as Cwa under the Köppen system (Alvares et al., 2013), characterized by a humid subtropical climate with dry winters and hot summers. Elevations in the study area range between 700 and 1,700 meters above sea level (Oliveira-Filho & Fontes, 2000).

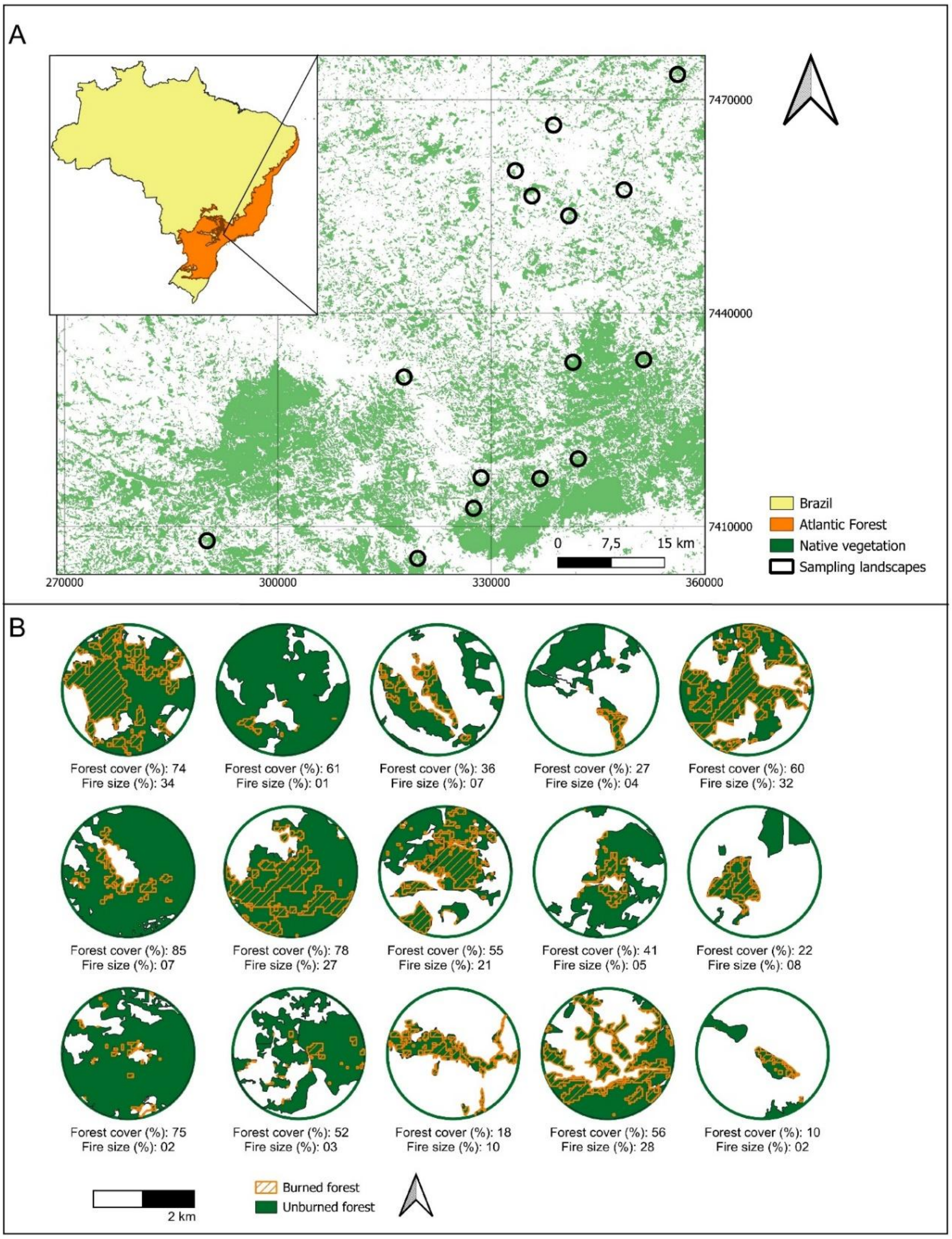


Figure 1: Study region containing the 15 sampling landscapes (black circles) in the Southeastern Brazilian Atlantic Forest (A). Sampled landscapes and their relative percentage of forest cover and burned area (B).

Study sites and landscape metrics

To identify fires and calculate their size and severity, we applied a five-step process. First, to evaluate the number of fires and determine their locations, we used the hotspot database of all satellites from the Institute for Space Research (INPE; available at https://terrabrasilis.dpi.inpe.br/queimadas/bdqueimadas), covering the period from 2013 to 2022 and filtered by the Atlantic Forest Biome within the state of São Paulo. These hotspots are vector point files corresponding to pixels with high temperatures detected by satellite sensors, serving as indicators of fire occurrences.

Second, we applied the delta Normalized Burn Ratio index (ΔNBR; derived from the Normalized Burn Ratio index; Table S1) to Landsat 8 images with a spatial resolution of 30 meters and low cloud cover, sourced from the United States Geological Survey's Earth Explorer (USGS, available at http://earthexplorer.usgs.gov). This index effectively maps the degree of environmental changes caused by fire (fire severity) across different forest types and geographical locations (Cocke et al., 2005; Lee et al., 2009). Positive ΔNBR values indicate improvements in post-fire vegetation conditions compared to pre-fire conditions, often associated with recovery and regrowth. Negative ΔNBR values suggest a decline in vegetation health, typically associated with increased burn severity and damage. To remove seasonal biases, we conducted biannual applications of this index, consistently covering the same time range as the hotspots (2013–2022). Each application was performed in both dry and wet seasons to select the image with the largest extent of burned forest. Fire severity was calculated using the mean ΔNBR values from both seasons.

Third, we reclassified the ΔNBR values as proposed by Keeley (2009) to distinguish between unburned and burned forests and to calculate fire sizes as a percentage relative to the landscape. Fire size and severity were calculated only for burned forests, disregarding other burned land covers. Landscapes that had burned again after the sampled fire were excluded from the analysis. Fire size proportions in our landscapes ranged from one to 34%. When possible, fire occurrences were also validated using high-resolution satellite images from the Google database from the year following the fire events, as well as fire occurrence reports from conservation units (Fig.S1A). Field validation was also conducted by observing physical evidence of fire (e.g., burned trees, open canopies) and through interviews with local residents (Fig.S1B and Fig.S1C).

After calculating the fire sizes, we created circular buffers with a 1 km radius around the fire centers to delineate our sampling landscapes. This scale was chosen based on evidence from previous studies in the region, which demonstrated that birds respond effectively to similar scales when evaluating taxonomic, functional, and phylogenetic diversity (Barros et al., 2019; Adorno et al., 2021; Manzoli et al., 2024). Within each landscape, we performed photointerpretation and delineation of native forest cover using high-resolution satellite imagery from 2022, available through the Google Earth database (Google, 2022). We then assigned a percentage value of forest cover to each landscape, creating a gradient ranging from 10% to 85% of forest cover.

To assess vegetation productivity, we used cloud-free Landsat 8 images, acquired from the USGS, from the rainy season of 2022 to calculate the normalized difference vegetation index (NDVI) for each study forest class at a 30 m resolution, applying the formula: NDVI = (NIR − red) / (NIR + red) (Marabel & Alvarez-Taboada, 2013). This calculation was based on imagery from the period in which bird sampling was conducted. NDVI is sensitive to photosynthetically active biomass and is positively correlated with plant productivity and resource availability (Pettorelli et al., 2005). NDVI values range from −1.0, representing non-vegetated surfaces such as water or barren rock, to 1.0, indicating maximum green vegetation. Consequently, higher NDVI values indicate areas with fully recovered above-ground biomass, characteristic of old-growth forests, while lower values suggest reduced photosynthetic activity due to canopy gaps, young regrowth, or extensive edge effects.

These processes resulted in the identification of 15 landscapes that burned in three different years (2014, 2020, and 2021; Fig. 1B). Explanatory analysis revealed no significant differences in bird diversity among these burn years. Consequently, we grouped these three years into a single forest category ("burned forest"). All study site selection and landscape metric characterization were conducted using QGIS software (version 3.22).

Bird sampling

Bird sampling was conducted across 15 landscapes between October 2022 and January 2023 using the fixed-point count method, which involves recording all bird species seen or heard within a 50-meter radius (Sutherland, 2006). In each landscape, we established four sampling points, divided evenly between unburned and burned forests. Points were arranged in pairs, with a minimum distance of 200 meters between them to avoid overlap and ensure independent sampling, as recommended by Vielliard et al. (2010). Each point was sampled twice on different days within the first three hours after sunrise. Only birds actively using the habitat were recorded (e.g., birds flying overhead were excluded). Sampling at each point lasted 20 minutes per visit.

For analysis, the two points within the same forest type in each landscape were considered subsamples, and their species occurrences were treated as repetitions. This resulted in a total of four repetitions per landscape (two points sampled twice). Each landscape was thus represented by one sample unit for each forest type (burned and unburned forests), amounting to 30 sample units across all landscapes. Each sample unit was observed for a total of 80 minutes. The abundance of each species in each subsample was determined as the highest count recorded during a single visit. The abundance for each sample unit was calculated as the sum of the abundances from its subsamples.

Given the high frequency of rare species in our study area, which increases the likelihood of non-detection during individual surveys, we applied an occupancy modeling approach using the 'unmarkedFrameOccu' function from the 'unmarked' package in R (Fiske & Chandler, 2011; Kellner et al., 2023). This approach allowed us to estimate the probability of species occupancy and to refine our estimate of species richness by counting only species with predicted occupancy values at or above a threshold of 1 (Royle et al., 2005). By accounting for imperfect detection, this method provided a more accurate estimate of species richness across our sampling points.

Bird species richness and functional diversity

For each bird community (sample units), we calculated the total species richness (total number of species) and functional diversity indices. To access functional diversity indices, we evaluated 12 bird traits corresponding to their sensitivity to disturbance and to their capacity to explore and use the environment and its resources (Flynn et al., 2009): diet, foraging stratum, forest affinity, nesting locality, body mass, beak length, beak width, beak depth, tarsus length, wing length, tail length and Kipp's distance (see more details in Table S2).

Functional diversity indices were derived using two matrices: a community matrix (sites × species abundances) and a trait matrix (species × traits). Given that our trait data includes both continuous and categorical variables (all weighted equally), we first calculated a Gower distance matrix from the trait data, yielding a species × species distance matrix. This matrix was then subjected to principal coordinates analysis (PCoA), producing a species × PCoA axes matrix. This matrix represents species distribution within a functional space with reduced, uncorrelated dimensions. By combining these species coordinates with the community matrix, we obtained four functional diversity indices for each of the 30 sampling points (Villéger et al., 2008), using the ‘FD’ package in the R Software (“dbFD” function) (Laliberté & Legendre, 2010):

Functional Richness (FRic): Quantifies the extent to which species occupy functional space in a community, serving as an indicator of potentially utilized or unutilized niche space. An increase in functional richness may reflect enhanced resource use efficiency (Mason et al., 2005; Villéger et al., 2008).

- Functional Evenness (FEve): Evaluates the distribution of species' traits within the occupied functional space. It assesses the degree to which traits are evenly distributed throughout the niche space. Lower FEve values indicate that certain parts of the niche space are underutilized, leading to reduced ecosystem functioning due to less efficient resource utilization (Mason et al., 2005).

- Functional Divergence (FDiv): Measures the relative abundance of species with unique traits, which can indicate a niche differentiation. Thus, low FDiv values represent a low abundance of species with unique traits, with possibly increased competition between species (Schleuter et al., 2010).

- Functional Dispersion (FDis): Measures the dispersion of species in the functional trait space as the mean distance of individual species to the centroid of all species (Laliberté & Legendre, 2010). Changes in functional dispersion indicate shifts in how species' traits deviate from the central point within the community's functional trait space.

Data analysis

We analyzed the species composition of bird communities in unburned and burned forests using non-metric multidimensional scaling (NMDS), based on Bray-Curtis dissimilarity indices calculated from the absolute abundance of each species in each sample unit (ter Braak et al., 1995; Gotelli & Ellison, 2011). To evaluate the statistical significance of differences in community composition between the two forest types, we applied a Permutational Multivariate Analysis of Variance (PERMANOVA) to the similarity matrix. This analysis was performed with 999 permutations and a significance level set at $\alpha = 0.05$. All analyses, including matrix construction, NMDS, and PERMANOVA, were conducted in R using the 'vegan' package.

To evaluate whether bird diversity is influenced by landscape features, we used generalized linear mixed models (GLMMs) implemented with the 'GlmmTMB' function from the 'glmmTMB' package (Brooks et al., 2017). The explanatory variables included native forest cover (%), vegetation productivity (mean NDVI), fire size (%), fire severity (mean ΔNBR), and forest type (unburned or burned). A Spearman correlation matrix of the initial explanatory variables indicated no collinearity issues ($p > 0.5$). We first constructed univariate models, each focusing on a single explanatory variable, and subsequently developed multivariate models with combinations of variables and their interactions to comprehensively assess their effects on bird diversity. To account for the nested structure of the data, we included landscape as a random factor. Model selection was based on the Akaike Information Criterion corrected for small sample sizes (AICc), identifying the most parsimonious model as the one with the lowest ΔAICc value (Martensen et al., 2012). Akaike weights were also calculated, with higher values (ranging from 0 to 1) indicating greater model support. Model comparisons, including ΔAICc values and weights, were performed using the AICtab function from the 'bbmle' package (Bolker, 2017). We assessed model adequacy by evaluating residual dispersion and distribution using the 'DHARMa' package in R (Hartig & Lohse, 2022).

Results

We sampled 182 bird species from 42 families across the 15 landscapes studied (Table S3). Species richness, grouped across all sampling points within each forest type, was nearly identical, with 149 species recorded in unburned forests and 148 in burned forests. The number of unique species was also similar between the two forest types, with 34 species exclusive to unburned forests and 32 to burned forests. Unexpectedly, our NMDS analysis indicated a similar bird species composition across both forest types (Fig. 2). Similarly, bird diversity—both species richness and functional—did not differ significantly between the treatments, as none of our models identified forest type as a significant predictor.

Our models confirmed our hypotheses related to bird responses to landscape features (Table 1). Species richness was best explained by the additive effect of forest type and vegetation productivity. Both unburned and burned forests showed a positive association with this variable, indicating that bird diversity responded similarly to vegetation productivity across forest types (Fig. 3A). Functional divergence was best explained by the interaction between forest type and fire size. The two forest types showed opposite response patterns: unburned forests displayed a positive association with fire size, while burned forests showed a negative association (Fig. 3B). Lastly, functional dispersion was best explained by fire size, showing a negative association with this predictor (Fig. 3C). Functional richness and functional evenness were not present in any valid model.

Table 1: Best model for each bird diversity index ranked by the lowest ΔAIC values with no residual problems.

Diversity indices	Models	AIC	dAIC	df	Weight	Significance
Species richness	~ Forest class + NDVI	211.8	1.3	4	0.17	Unburned forest = 0.25 **NDVI = 0.001****
Functional divergence	~ Forest class * Fire size	-114.4	0	6	0.20	**Unburned forest = 0.001 **** Fire size = 0.33 **Unburned forest:Fire size = 0.001 ****
Functional dispersion	~ Fire size	-51.1	0	4	0.28	**Fire size = 0.027 ***

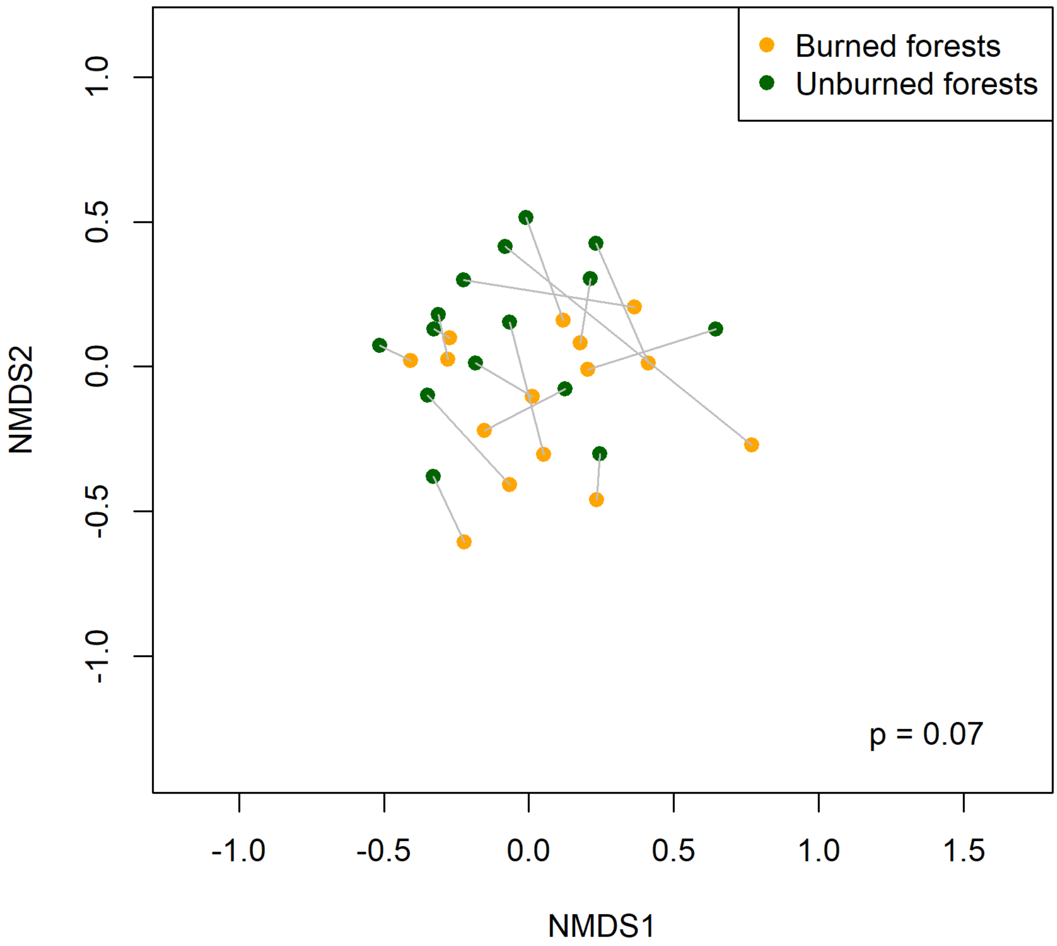


Figure 2: Results of the NMDS analysis of the species composition of unburned (green dots) and burned forests (orange dots) surveyed during the present study. Lines link the forest types from

the same sampling landscapes.

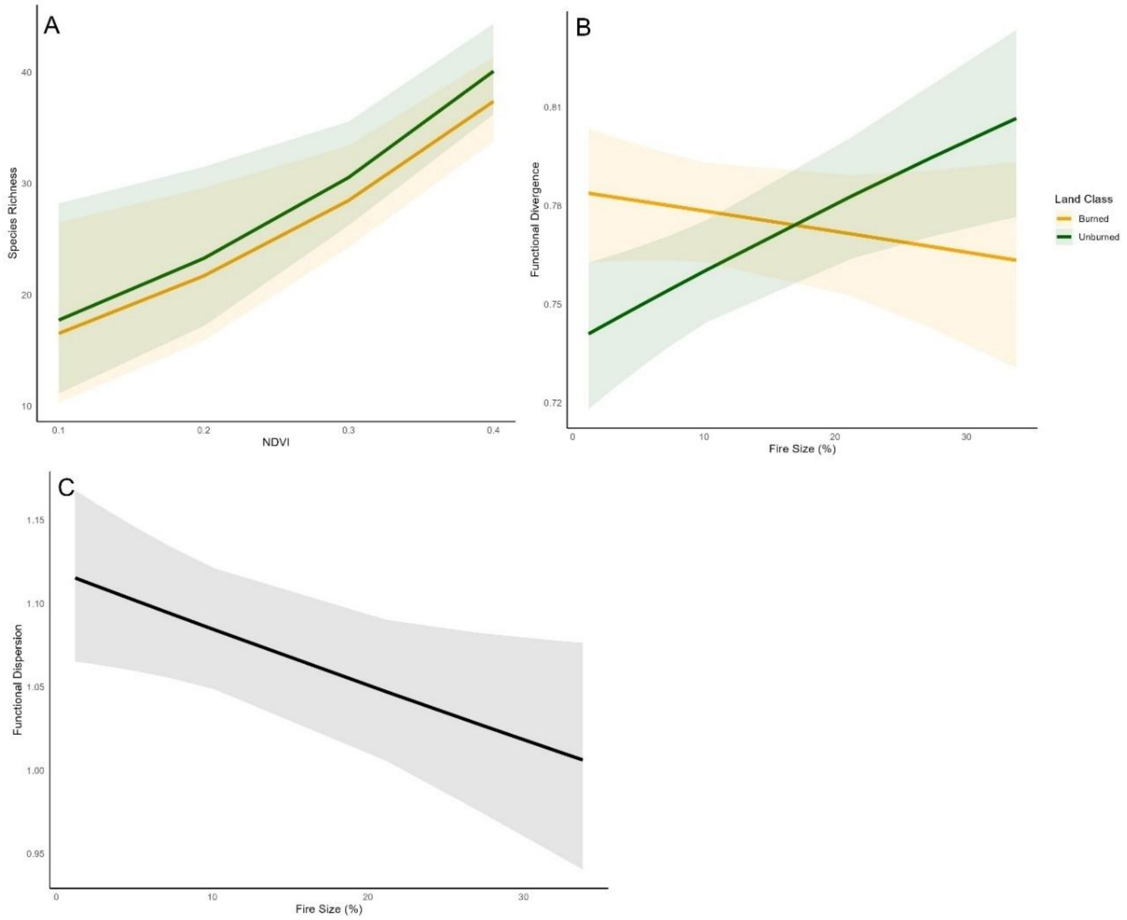


Figure 3: Predicted responses of bird communities to vegetation productivity (A) and fire size (B and C) within burned landscapes of the Brazilian Atlantic Forest (N=15).

Discussion

This study is among the first to assess fire impacts on bird diversity in the Atlantic Forest, a highly deforested tropical biome. It provides new evidence for bird conservation in response to increasing fire activity in this region, which has received less attention compared to the Amazon. We found that bird communities in unburned and burned forests were similar in both composition and diversity, a result that contrasts with findings from most studies conducted in Amazonian forests. As predicted, bird diversity can be explained by vegetation productivity and fire size. However, these responses can vary depending on the diversity metric used (species richness or functional indices) and on whether the forest was burned or not.

Patterns of similarity between unburned and burned forests

The similar composition of bird communities between forest types in our study area contrasts with findings from central Amazonia. In Amazon forests, fire events often lead to the replacement of disturbance-sensitive and habitat-specialist bird species by more common, disturbance-tolerant, and habitat-generalist species (Barlow et al., 2002; Barlow & Peres, 2004; Mestre et al., 2013). We attribute these differences among regions to two main reasons. First, the time elapsed between the fire and our sampling was sufficient for the vegetation to recover to a point where it no longer acted as an ecological barrier for birds (Haugaasen et al., 2003). Hence, the short distance between unburned and burned forests in our study region likely facilitates species dispersal and colonization, a process that have already been found in the western Amazon (Barlow et al., 2012; Lemos da Silva et al., 2015). Second, differences in landscape context and historical patterns of land use between the Amazon and Atlantic Forests likely contribute to the contrasting bird responses observed (Brondízio, 2006; Ribeiro et al., 2009). Unlike the Amazon, where large expanses of continuous forest still dominate, the Atlantic Forest is highly fragmented, with much of its native vegetation reduced to small, isolated patches. These patches are often composed of secondary, degraded forests that experience strong edge effects and other anthropogenic pressures (Ribeiro et al., 2009). This hyper-fragmentation has likely led to the exclusion of many disturbance-sensitive and habitat-specialist bird species over time, independent of the effects of fire (Oliveira et al., 2020; Tabarelli et al., 2010). This historical context underscores the need for careful interpretation when comparing post-fire responses across distinct biomes, as landscape-level and historical factors likely play a critical role in shaping species resilience and community structure.

Conversely, the similar levels of species richness and functional diversity observed between forest types align with findings from studies conducted in the western and central Amazon (Barlow et al., 2002; Barlow et al., 2004; Hidasi-Neto et al., 2012; Mestre et al., 2013; Barlow et al., 2012; Lemos da Silva et al., 2015), suggesting that this pattern may be consistent across Brazilian tropical forests. However, unlike Amazonian forests, the similarity in diversity between unburned and burned communities is not driven by species replacement. Moreover, it is important to highlight that our sampling design did not include forests that experienced multiple fires since 2014. If the Atlantic Forest follows patterns observed in the Amazon, species richness may diverge between unburned and burned forests as fire frequency increases (Barlow & Peres, 2004; Silveira et al., 2016). Future research should explore bird responses in areas subjected to recurrent burns to provide a more comprehensive understanding of the effects of fire on bird diversity in the Atlantic Forest.

Bird responses to landscape features

The observation that species richness did not differ between unburned and burned forests, yet both were positively associated with vegetation productivity, suggests that fire itself was not the primary driver of these indices. Instead, vegetation structure and resource availability, as reflected by NDVI, appear to play a more critical role in shaping taxonomic diversity across forest types. This correlation aligns with the species-energy hypothesis (Evans et al., 2005), which posits that areas with higher primary productivity sustain greater diversity by providing increased resource availability (Radeloff et al., 2019; Rowhani et al., 2008). These findings are further supported by fire-related studies in the Amazon, where local forest structure (e.g., canopy openness and understory vegetation) has been shown to be a stronger predictor of bird responses than fire treatment alone (Barlow et al., 2002; 2004; Hidasi-Neto et al., 2012; Silveira et al., 2016). While NDVI serves as a reliable indicator of vegetation quality (Pettorelli et al., 2005), our study did not assess specific local vegetation characteristics. Addressing this limitation in future research on fires in the Atlantic Forest will be crucial for producing more precise and nuanced ecological insights.

Both FDiv (i.e., functional divergence) and FDis (i.e., functional dispersion) demonstrated a negative correlation with fire size, with FDiv showing this trend in burned forests (although not statistically significant) and FDis reflecting it across combined forest types (burned and unburned forests). This suggests that larger fire events lead to communities with more homogenized functional traits, where species tend to cluster around central functional niches, indicating reduced functional diversity and dispersion (Hidasi-Neto et al., 2012; Mouchet et al., 2010). Such patterns may reflect environmental filtering imposed by fire, selecting species with specific life-history traits (Barnagaud et al., 2014; Newbold et al., 2013). The likely explanation for this environmental filtering lies in the significant changes to vegetation structure caused by large fires. These include the mortality of fire-sensitive tree species and their replacement by fast-growing shrubs and herbaceous plants, which drastically alter habitat availability and quality for birds (Barlow & Peres, 2004; Turner et al., 1997). Moreover, as fire size increases, undisturbed patches within the forest become more isolated, leading to greater landscape fragmentation. This growing isolation among bird communities reduces connectivity, limiting dispersal opportunities for specialist species while favoring generalists that thrive in degraded or simplified habitats (Banks-Leite et al., 2014; Steel et al., 2022). Although we did not observe similar species composition between unburned and burned areas, our results suggest that this similarity may not occur along the fire size gradient.

Larger fires create extensive edge habitats between unburned vegetation and patches with varying fire severity (Steel et al., 2018). These spatial discontinuities act as 'keystone structures' in mosaic landscapes, offering complementary and supplementary resources that support species with distinct life-history traits (Barbaro & Van Halder, 2009; Tews et al., 2004). This process likely explains the positive correlation between fire size and FDiv in unburned forests. In this context, unburned forests within landscapes affected by larger fires may support a higher abundance of bird species with unique traits (Schleuter et al., 2010). While previous studies have shown that spatial variation in fire patterns enhances bird taxonomic diversity (Steel et al., 2022), our findings extend this relationship to functional diversity metrics. This underscores the importance of incorporating functional indices to fully capture the broader ecological impacts of fire on bird communities, even in unburned areas.

Management implications

Understanding fire impacts on bird communities is crucial for effectively managing fire-sensitive ecosystems and conserving biodiversity. Our findings have several implications for the conservation and management of burned landscapes within the Atlantic Forest. Given that bird species richness is influenced by vegetation productivity, conservation efforts should focus on strategies that enhance vegetation productivity to support the highest number of species. Such strategies may include increasing native vegetation cover and restoring degraded forests (Pizo & Tonetti, 2020). Promoting higher productivity across entire landscapes could also be achieved through the establishment of high-productivity tree plantations managed with low-intensity practices (Lopes et al., 2015; Pizo & Tonetti, 2020). Additionally, simpler measures like fencing forests to prevent the invasion of domestic animals, such as cattle, could mitigate soil compaction, forest degradation, and hindered natural regeneration (Paulo & Almeida, 2016; Samojlik et al., 2016). Although species richness responds more strongly to productivity than to fire, conservation programs should also prioritize fire prevention, as recurring disturbances can significantly reduce vegetation productivity and habitat quality (Saha et al., 2023).

Given that large fires can lead to the homogenization of functional traits, implementing fire prevention and control measures is crucial to preserving a broader spectrum of avian functional traits. Although the New Brazilian Forest Code includes a dedicated chapter on fires, the Atlantic Forest continues to experience a significant number of fire incidents, raising concerns about the code's effectiveness (Nascimento et al., 2022). Recently, the federal government introduced the National Action Plan for the Conservation of Atlantic Forest Birds (Chico Mendes Institute for Biodiversity Conservation, 2023), which aims to protect, restore, and expand bird habitats within the biome. However, the plan offers limited discussion on the effects of fire and strategies to address this disturbance. We propose that such strategies should incorporate a ‘fire-smart management’ approach, which emphasizes managing the entire landscape to reduce fire risk (Pivello et al., 2021). In this context, establishing low fire-risk matrices composed of land uses less prone to fire around forests could be an effective strategy to prevent fire spread (Carmo et al., 2011b). Finally, the Atlantic Forest would benefit from implementing programs dedicated to forecasting and monitoring wildfires, similar to those established for the Amazon. Fire prevention and mitigation plans should be developed proactively, prioritizing high-risk areas identified through deforestation alerts (Pivello et al., 2021).

Conclusions

To date, this is the first study to evaluate the impacts of fire on bird communities within the Atlantic Forest and one of the few to assess fire impacts on functional diversity worldwide. Despite similarities in composition, species richness and functional diversity between unburned and burned forests, the observed patterns underscore the critical role of vegetation productivity and fire size in shaping bird communities. These results emphasize the importance of landscape-level and historical factors, such as hyper-fragmentation and land-use legacies, in influencing post-fire ecological dynamics. Our findings have important implications for conservation and management. Enhancing vegetation productivity through forest restoration, promoting sustainable land-use practices, and implementing robust fire prevention strategies are essential to maintaining biodiversity in this fire-sensitive biome. Additionally, given the potential for large fires to homogenize functional traits and reduce habitat quality, adopting a fire-smart management approach that incorporates proactive mitigation, monitoring, and the creation of fire-resistant landscapes is paramount. These strategies must be supported by active governmental policies focused on preventing and controlling fires to ensure the long-term conservation of Atlantic Forest biodiversity.

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