

UNIVERSIDADE FEDERAL DE MINAS GERAIS

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Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre

Juliana Kuchenbecker Belisário

**DISTRIBUIÇÃO ESPAÇO-TEMPORAL DE INSETOS HERBÍVOROS
EM ILHAS DE FLORESTAS NATURAIS ALTIMONTANAS SOB
DISTÚRBIOS ANTRÓPICOS**



BELO HORIZONTE

2022

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Co-orientadores: Dr. Marcílio Fagundes

Dr. Luiz Eduardo Macedo Reis

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Ata da Defesa de Tese

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No dia 16 de dezembro de 2022, às 14:00 horas, por vídeo conferência, teve lugar a defesa de tese de doutorado no Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, de autoria do(a) doutorando(a) Juliana Kuchenbecker Belisario, orientando(a) do Professor Frederico de Siqueira Neves, intitulada: "**Distribuição espaço-temporal de insetos herbívoros em ilhas de florestas naturais altimontanas sob distúrbios antrópicos**". Abrindo a sessão, o(a) Presidente(a) da Comissão, Doutor(a) Frederico de Siqueira Neves, após dar a conhecer aos presentes o teor das normas regulamentares do trabalho final, passou a palavra para o(a) candidato(a) para apresentação de seu trabalho. Estiveram presentes a Banca Examinadora composta pelos Doutores: Lucas Navarro Paolucci (UFV), Milton Barbosa da Silva Júnior (UFMG), Reuber Lana Antoniazzi Júnior (Stephen F. Austin State University), Ramiro Aguilar (Universidad Nacional de Córdoba) e demais convidados. Seguiu-se a arguição pelos examinadores, com a respectiva defesa do(a) candidato(a). Após a arguição, apenas os senhores examinadores permaneceram no recinto para avaliação e deliberação acerca do resultado final, sendo a decisão da banca pela:

(X) Aprovação da tese, com eventuais correções mínimas e entrega de versão final pelo orientador diretamente à Secretaria do Programa, no prazo máximo de 30 dias;

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A banca indica esta tese aos Prêmios CAPES e UFMG de teses? (X) SIM () NÃO

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Belo Horizonte, 16 de dezembro de 2022.

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O conhecimento isolado é lâmpada sem proveito; contudo, transitado de cérebro a
cérebro é ciência e cultura.

Emmanuel

Resumo

Compreender os padrões espaço-temporais e os mecanismos que estruturam as metacomunidades de insetos herbívoros associados às ilhas de floresta natural da Serra do Espinhaço foi o principal objetivo desta tese. No primeiro capítulo, mostramos que fatores espaciais e temporais têm contribuições mistas para a diversidade e distribuição de insetos herbívoros, onde a grande mudança na composição de espécies foi especialmente moldada por variações sazonais nas características climáticas. No segundo capítulo, destacamos a complexidade dos resultados de distúrbios como a incidência de fogo e o pastoreio de gado no sistema de estudo, enfatizando o fogo como uma grande ameaça, mas também indicando surpreendentemente que o pastoreio do gado pode mitigar os efeitos negativos do fogo nas ilhas florestais sensíveis ao fogo. No terceiro e último capítulo, avaliamos a influência desses dois distúrbios, juntamente com propriedades locais das ilhas florestais, na distribuição espaço-temporal de insetos herbívoros ao longo dos anos. Evidenciamos o fogo como a única variável que influencia a estabilidade dos insetos herbívoros, e a variação da cobertura do dossel como a única variável que explica os processos de ganhos e perdas de espécies. Compreender a dinâmica subjacente à estabilidade das metacomunidades de insetos fornece uma maneira robusta de prever como a organização da biodiversidade e a funcionalidade do ecossistema mudarão em resposta a outras mudanças ambientais e climáticas, que são mais pronunciadas em áreas de alta altitude.

Palavras-chave: *campo rupestre*; Espinhaço; estrutura de comunidades; fogo; gado; ilhas florestais; insetos herbívoros; metacomunidades; padrões espaço-temporais; β -diversidade

Abstract

Understanding the spatiotemporal patterns and the mechanisms that structure herbivorous insects' metacommunities associated with natural forest islands of the Espinhaço Range was the main objective of this thesis. In the first chapter, we showed that both spatial and temporal factors have mixed contributions to herbivorous insects' diversity and distribution, where the great change in their composition was especially shaped by seasonal variations in climatic characteristics. In the second chapter, we highlighted the complexity of the outcomes of disturbance by fire and large grazers in the study system, emphasizing fire as a major threat but also surprisingly indicating that cattle grazing can mitigate the negative effects of fire on the fire-sensitive forest islands. In the third and final chapter, we evaluated the influence of these both disturbances, along with local properties of the forest islands, on the spatiotemporal distribution of herbivorous insects over years. We evidenced fire as the only variable influencing the stability of herbivorous insects and the canopy cover variation as the only one explaining species gains and losses. Comprehending the dynamics underlying the stability of insect metacommunities provides a robust way to predict how the organization of biodiversity and ecosystem functionality will change in response to further environmental and climatic changes, that are more pronounced in high-elevation areas.

Keywords: *campo rupestre*; cattle; community structure; Espinhaço; fire; forest islands; herbivorous insects; metacommunities; spatiotemporal patterns; β -diversity;

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General introduction

Islands have fascinated humans for millennia. It was just in the 60s that they received their due recognition with the emergence of the Theory of Island Biogeography by MacArthur and Wilson (MacArthur and Wilson, 1967). This Theory served as a basis and stimulus for understanding the processes that determine the spatial distribution of all biological diversity. It also has been widely used to assimilate and interpret the biodiversity dynamics in fragmented terrestrial habitats (Yekwayo et al. 2016). Although human-fragmented areas are extensively studied (see Cook et al., 2004; Smedt et al., 2019), few studies have been carried out on natural forest fragments immersed in an adjacent more open landscape (but see Driscoll, 2008; Neves et al., 2021). These naturally fragmented terrestrial landscapes are exceptionally valuable as they allow us to comprehend how species behave and how they are distributed without having to consider any disturbance related to human-caused habitat loss. In this regard, the *Capões de Mata* of the Espinhaço Mountain Range represent excellent models for testing ecological hypotheses, since they have reduced dimensions, different degrees of isolation, and well-defined borders (Coelho et al., 2017).

The Espinhaço formation is an important mountainous formation in Brazil due to its high biodiversity and endemism (Silveira et al., 2016; Miola et al., 2021). It extends almost continuously for 1200 km from northeastern to southeastern Brazil, across two states, Bahia and Minas Gerais. This mountain chain also acts as a humidity barrier between two biomes, the Cerrado (Brazilian savannah) to the west and the Atlantic Forest to the east. Above 900 m. a.s.l. in this region a continuous open grassland matrix called *campo rupestre* is predominant. In the *campo rupestre* matrix there are some forest islands called *Capões de Mata* that merge as natural patches of vegetation from mountaintops. The *Capões de Mata* occur mainly at 1200 m a.s.l. and their maintenance is dependent on specific climate and soil properties (see Coelho et al., 2016 for a review). These environments are characterized by a floristic composition similar to seasonal semi-deciduous forests associated with the Atlantic Forest domain (Coelho et al., 2016, 2018). The species composition includes families with wide geographical distributions, although many species are largely endemic and reveal the former isolation of this refuge, which can also be known as *cloud forest*, *dwarf forest*, *montane rainforest*, among others (see Stadtmüller, 1987; Hamilton et al., 1995b; and Foster, 2001 for a detailed account of used nomenclature). Compared with lowland forests, the *Capões de Mata* have a lower canopy

and a greater abundance of epiphytes, with a significant representation of Araceae, Orchidaceae, Bromeliaceae, Pteridophyta, and Bryophyta (Coelho et al., 2018). This elevated representativeness of epiphytes is a consequence of the high humidity in these formations (Whitmore, 1990; Van der Hammen, 1995; Webster, 1995). Indeed, in the Espinhaço range's high elevations the relative humidity is always high due to the nebular condensation of humid air (Coelho et al., 2016), but the temperature varies seasonally, with a mean difference of 4.54°C between seasons (see Silveira et al., 2019).

The importance of the *Capões de Mata* goes far beyond being natural islands that host an extremely rich biodiversity, contributing to the high diversity pattern of tropical mountaintops (Perrigo et al., 2020). We can consider these environments as real reservoirs of forest biodiversity, sheltering a large number of species that would be doomed to disappear. This is especially true during periods of rapid climate change, because species need to move shorter distances along a mountain gradient to find their optimal niches compared to lowlands (Chen et al., 2011; Sandel et al., 2011). Additionally, this ecosystem is generally associated with headwaters and small streams (Coelho et al., 2016), and protects two of the three main Brazilian hydrographic basins (Callisto et al., 2019). Thus, strategies for preserving and maintaining these particular forest islands must be at the top priorities of conservation plans and policymakers.

Few groups of organisms have data collected in *Capões de Mata*. Much of the knowledge about the invertebrate fauna of the *Capões de Mata* associated with the open grasslands of Espinhaço Range comes from the Long-Term Ecological Projects in Serra do Cipó, Minas Gerais (PELD-CRSC/CNPq). In these projects, insects dominate as the most frequent object of study (see Pereira et al., 2017; da Silva et al., 2019; Perillo et al., 2019; Castro et al., 2020; Brant et al., 2021; Neves et al., 2021). In addition to responding to changes in the environment, insects are easily collected, have a short generation time, and are usually very abundant. Particularly, herbivorous insects account for a large part of the total insect abundance, living among plant species in search of food resources. In fact, insect-dominated plant-based food webs constitute an estimated 75% of global terrestrial biodiversity (Price, 2002; Mora et al., 2011). Therefore, studying herbivorous insect distribution and diversity patterns is fundamental to understanding how global biodiversity is formed, although there is still a large gap in ecological and conservation studies.

Island flora and associated herbivorous insect fauna have fewer possibilities for survival when overwhelming events occur, despite habitat heterogeneity (Whittaker, 1995; Taylor and Kumar, 2016). In spite of it, the *Capões de Mata* are facing increasing anthropogenic threats which can severely alter their entire dynamics and balance (Pereira et al., 2017; da Silva et al., 2019). For instance, fire events have been frequently invoked as a major factor shaping forest-grassland mosaics in tropical mountains (Pausas and Bond, 2020). A fire in a forest can convert a closed habitat into a completely open one, disconnecting canopies and altering the microclimate conditions along the vertical strata (Abreu et al., 2017; Andersen, 2019). Importantly, this disturbance might be particularly strong for the herbivorous insect species living in the understory of forests, where the changes in the structure of plant communities can be even more drastic compared to the canopy (Vogel et al., 2010). Thus, understanding how herbivorous insect communities respond to burning in space and time is primordial for better accounting for conservation needs in greater detail for complex and vital environments.

While the role of fire has been more often studied in forest-grassland mosaics (Flores et al., 2021), the role of large herbivores in driving the distribution of tropical biomes has received less attention. Nevertheless, evidence suggests that large mammal herbivores are key players in plant evolution and vegetation patterns (Baggio et al., 2021; Dantas and Pausas, 2022; Overbeck et al. 2022; Durigan et al., 2022). The significant observed effects of cattle grazing on plant-herbivorous insect network are mostly due to trampling and the consumption of flowers and sprouts that promote vegetation community compositional shifts and, ultimately, the alteration of its structure (Fleischner, 1994; Daskin et al., 2016). Actually, some studies have demonstrated that cattle grazing changes the structure of herbivorous insect communities even after many years (Daskin et al., 2016). Herbivorous insect species that exclusively depend on understory vegetation to explore resources to nest, forage, and feed are likely to be much more negatively affected by cattle grazing than the ones that forage predominantly in the canopy. In this way, spatial context is critical when evaluating the impact of anthropic disturbances, such as cattle grazing, on the functioning and dynamics of tropical ecosystems with forests with well-defined spatial structures.

The challenge of this thesis is to deepen the knowledge about how metacommunities of herbivorous insects are structured and organized in the *Capões de*

Mata associated with Serra do Espinhaço. We intend to understand the spatio-temporal patterns and mechanisms that determine the diversity and distribution of this insect fauna in these highly threatened natural environments. Additionally, we also intend to comprehend how anthropic disturbances, such as the incidence of fire and the presence of cattle, influence over time both the herbivorous insects and the *Capões de Mata* at a local and landscape scale. For that, we divided this thesis into three chapters, using different scales and approaches. In the first chapter, we aimed to explore the spatiotemporal patterns of herbivorous insect diversity using three spatial and one temporal scale. In the second chapter, we aimed to determine how fire and cattle grazing drive variation in canopy cover and landscape properties in the *Capões de Mata*. For the third and final chapter, our objective was to understand whether the metacommunity stability of herbivorous insect species is influenced by canopy cover variation and/or anthropic disturbances over time in the studied system.

We present below the three chapters, written in English and complying with the formatting required for each scientific journal in which the article was published or intended for submission. Also, we include as an attachment the cover of the first published chapter (Appendix I), and four more indirect products of the thesis. Appendix II is an article published in Portuguese on the December 2021 edition of the special volume PELD–CRSC Newsletter, addressing the importance of monitoring the spatial and temporal dynamics of herbivorous insects in the *Capões de Mata*. Appendix III is a text published also in Portuguese on a conservation website (Bocaina Biologia da Conservação) about the same studied system and its main threats. Appendix IV is a video published on Youtube as part of the Method and Scientific Communication class during the content production exercise, where the candidate introduces the study system and all its importance. Finally, Appendix V is a video published also on Youtube, where the candidate, along with an exchange of professors from Brazil and Namibia, emphasize the importance of the studied system as a whole and the urgency of its preservation.

CHAPTER 1

Spatiotemporal distribution of herbivorous insects along always-green mountaintop forest islands



Juliana Kuchenbecker, Luiz Eduardo Macedo-Reis, Marcílio Fagundes, Frederico S. Neves

Keywords: Atlantic Forest; *campo rupestre*; chewing insects; fluid-feeding insects; xylophagous insects; β -diversity

Abstract

Insects make up the bulk of terrestrial diversity and about half of insect species are herbivores that have direct relationships with their host plants and are the basis of the entire food chain, on which wildlife and humanity depend. Some herbivorous insect traits, such as their spatio-temporal distribution, are especially relevant in the current scenario of global changes, which are more pronounced in high elevation areas, helping to improve the effectiveness of conservation actions. Here we evaluated the influence that different spatiotemporal scales have on three free-feeding herbivorous insect guilds (fluid-feeding, leaf-chewing and xylophagous insects) in montane forest islands immersed in a

grassland-dominated matrix (*campo rupestre*). We assessed whether species turnover or nestedness was the main component determining both spatial and temporal species composition variation (β -diversity) of the herbivorous insect community. We also checked the temporal effect on herbivorous insect guilds composition between vertical strata. We sampled herbivorous insects during two summers and two winters in 14 forest islands of different sizes and shapes in a natural mountainous fragment located in southeastern Brazil. A total of 6597 herbivorous insects representing 557 morphospecies were sampled, 290 of which were fluid-feeding, 147 leaf-chewing and 120 xylophagous insects. We found a main contribution of time scale in the organization of the herbivorous insect composition sampled in this study, mainly by turnover, with small differences among guilds. Additionally, we could see that climate determined the local variation of species, corroborating that we have a highly variable always-green system over space and time where the understory community varies less in comparison to the canopy community. Our findings suggest that long-term ecological research on herbivorous community structure in relation to climatic variation is a key element for future investigations, which can be decisive for the conservation of herbivorous insect communities. We also suggest that the effects of anthropogenic pressures must be monitored in this system, since these forest islands may serve as warming refuges in a fragmented landscape holding an invaluable diversity of species that, without these old-growth forest reservoirs, would be doomed to disappear.

1 Introduction

Insects make up the bulk of terrestrial diversity (Sabrosky, 1953; Chapman, 2009; Stork, 2018), being considered the most important animals in terrestrial environments (Wilson, 1987). However, recent case studies have shown drastic declines in the total biomass of different insect groups (Schuch et al., 2012; Dirzo et al., 2014; Hallmann et al., 2017; Lister and Garcia, 2018), which can lead to the loss of multiple critical ecosystem services provided by them (e.g., pollination and decomposition) (Ashton et al., 2021). Out of their vast numbers, about half are represented by herbivorous insects that have direct relationships with their host plants (Stork, 2018) and are the basis of the entire food chain, on which wildlife and humanity depend (Cardoso et al 2020). Many feeding guilds have evolved among herbivorous insects (e.g., fluid-feeding, leaf-chewing and xylophagous

insect guilds), with high variability in spatio-temporal distribution (Neves et al., 2014; Kuchenbecker and Fagundes, 2018; Macedo-Reis et al., 2019). Several works report the distinction between some different guilds and the importance of working with each one (see Novais et al., 2018; Monteiro et al., 2020). Changes in habitat characteristics, such as vegetation structure and climatic variations, determine the organization of these guilds in different ways, and changes in the herbivore community have substantial effects on biological interactions throughout the food chain (Leal et al., 2016; Novais et al., 2016, 2019). In addition, some herbivorous insect traits, such as their spatio-temporal distribution (Lewinsohn et al., 2005), are especially relevant in the current scenario of global changes that are more pronounced in high elevation areas (Janzen and Hallwachs, 2019), helping to improve the effectiveness of conservation actions (Cooke et al., 2013; Callisto et al., 2019).

Interpreting the diversity distribution patterns of different herbivorous insect feeding guilds enables us to understand the influence of distinct ecological processes structuring herbivorous insect communities (see Novotny and Weiblen 2005; Wardhaugh 2014). Since tropical rainforests are notoriously heterogeneous environments (Basset et al., 2012; Kitching et al., 2013), one of the obvious spatial gradients of species diversity change is related to geographic distance. Insect diversity changes in this horizontal dimension may be driven by multiple factors, including the distance among habitat patches or even the distance of these patches to a continuous forest (e.g., da Silva et al., 2019). In addition, dispersal abilities of herbivorous insects differ among guilds, which may potentially influence them to move in different ways within and among habitats (Tews et al., 2004; Macedo-Reis et al., 2019). Seasonal variability is also common in tropical environments, especially with regard to species composition (Tylianakis et al., 2005), which is affected by resource availability (Shaw, 2004; Inclán et al., 2014) and can be guild-dependent. With a few notable exceptions (see Macedo-Reis et al., 2016, 2019), temporal patterns of insect diversity that reflect seasonal climatic conditions are frequently ignored in tropical rainforests (Didham and Springate, 2003). Particularly, in seasonal environments, both spatial and temporal patterns among herbivorous insects need more attention in order for us to understand these diversity patterns.

Naturally-fragmented landscapes are exceptionally adequate for evaluating patterns and mechanisms that determine the distribution of species in environments

without confounding effects of human-driven fragmentation and habitat loss (Fahrig, 2017; Haddad et al., 2017). Unlike oceanic islands, which are surrounded by a matrix that is a barrier to most terrestrial fauna, forest islands have more permeable matrices that harbor an important percentage of fauna (Cook et al., 2004; Driscoll, 2005; Yekwayo et al., 2016) and provide additional resources to species (Öckinger et al., 2012). In such systems, that occur immersed in grassland-dominated ecosystems on tropical mountaintops (Streher et al., 2017), vagile organisms like wasps, bees, dung beetles and fruit-feeding butterflies can seek different resources (da Silva et al., 2019; Perillo et al., 2020; Silva et al., 2020), where habitat diversity and configuration of the landscape may elicit different responses among them (Neves et al., 2021). Although the distribution of host plants at a given scale represents food resource availability and physical structure for herbivorous insects to find shelter and breeding sites (Lewinsohn and Roslin, 2008), evidence of this relationship in forests patches at landscape scales and its effects on herbivorous insect communities is still poorly documented (Rossetti et al., 2019).

There is a substantial change in habitat conditions between understory and canopy strata (Shaw, 2004; Basset et al., 2015), and this vertical stratification is often considered to be a key factor promoting the extreme diversity of tropical forests (Oliveira and Scheffers, 2019). This is mainly because vertical stratification is associated with major shifts in abiotic conditions, highlighting the great variety in resource availability that enables greater species coexistence at small scales (Brown, 1981; Scheffers et al., 2017). In fact, herbivorous insect diversity changes in this vertical dimension may be driven by factors such as resource quantity and quality and microclimate conditions (DeVries et al., 1999; Basset et al., 2001, 2003a,b; Brehm, 2007) and they usually show a clear stratification that decreases from the canopy to lower strata (Basset et al., 1992, 2003a,b; Neves et al., 2014). Nevertheless, few studies have investigated whether local patterns of species diversity are related to vertical stratification of different insect feeding guilds, which may be more informative regarding the functional role of arthropods in tropical forests (but see Grimbacher and Stork, 2007; Neves et al., 2014). Furthermore, along with the increasing interest in canopy ecosystems (Nadkarni et al., 2011; Silva et al., 2017; Swart et al., 2020), here we simultaneously measured herbivorous insect species diversity in both canopy and understory environments through time to contribute to the current knowledge on the subject (De Vries, 1988; Wolda, 1992; Skvarla et al., 2021).

The joint use of multiple scales (α -, β - and γ -diversities; Whittaker, 1960) as well as a complimentary process-focused approach to decompose β -diversity into turnover (species substitution) and nestedness (a gradient of number of species) is an adequate framework to further advance our knowledge about how communities are structured in space and time, and the underlying mechanisms driving diversity patterns (Baselga, 2010). Indeed, species turnover has consistently been reported as the main component of total β -diversity for a wide range of taxa across different ecosystems (Soininen et al., 2018), and is a recurrent feature among insect communities (Leal et al., 2016; Silva et al., 2017; Macedo-Reis et al., 2019). However, such studies are still very necessary because distribution patterns vary with the scale of observation, which can range from centimeters to kilometers and from days to years (Allan and Castillo, 2007). Thus, it is important to assess both the horizontal and vertical spatio-temporal β -diversity in order to understand the mechanisms that determine the organization of insect communities, especially in megadiverse environments such as tropical forests.

Since global change would lead to multifaceted ecosystem modifications, including shifts in species distribution ranges and diversity (Chen et al., 2011) and other unpredictable cascading effects at different levels of ecological organization (Peñuelas et al., 2013), here we aimed to explore the spatiotemporal patterns of herbivorous insect diversity (i.e., richness, abundance and composition) in forest islands in a mountain range in eastern South America (Coelho et al., 2016). Four spatiotemporal scales were considered: three spatial scales (within Malaise traps; between strata of vegetation within forest sites; and among forest islands within sampling dates) and one temporal scale (over 4 sampling dates). We then tested (i) whether different spatiotemporal scales contribute in a different way to the diversity of three herbivorous insect guilds (i.e. fluid-feeding, leaf-chewing and xylophagous) in the forest islands; (ii) whether the variation of species composition over four seasons (spatial and temporal β -diversity) is determined by substitution (turnover) and (iii) whether the temporal variation of species composition (temporal β -diversity) varies between the vertical strata and among guilds. Specifically, we expect that:

- i. Spatial scale has the main contribution to the total diversity of herbivorous insects, since the forest islands are of different sizes, shapes and distances to the nearest island or to the continuous forest (Coelho et al., 2018) and the

canopy faces higher levels of UV radiation, wind speed and variations in humidity and temperature than the understory (Basset et al., 2003a);

- ii. Species turnover among sites is more important than nestedness in determining community organization within a region, as nestedness patterns are considerably less common to herbivorous insects in fragmented habitats (Macedo-Reis et al., 2019);
- iii. Canopy presents the higher variation in species composition (temporal β -diversity) for all three herbivorous insect guilds, as canopy environmental conditions and resource availability vary more than in the understory (Basset et al., 2003a).

2 Materials and methods

2.1 Study area

We conducted this study in a natural forest archipelago situated in Serra do Cipó (the southern portion of the Espinhaço Range), Minas Gerais state, southeastern Brazil (19°14'19"S, 43°31'35"W; Fig. 1). The Espinhaço formation is an important mountainous formation in Brazil due to its high biodiversity and endemism (Silveira et al., 2016; Miola et al., 2020). It extends almost continuously for 1200 km from northeastern to southeastern Brazil, across two states (Bahia and Minas Gerais), and acting as a humidity barrier between two biomes, the Cerrado (Brazilian savannah) to the west and the Atlantic Forest to the east. Above 900 m. a.s.l. in this region a continuous grassland matrix called *campo rupestre* is predominant. In the *campo rupestre* matrix there are some forest islands that merge as natural patches of vegetation from mountaintops. These forest islands occur mainly at 1200 m a.s.l. and their maintenance is dependent on specific climate and soil parameters (see Coelho et al., 2016 for a review). They have a floristic composition similar to seasonal semi-deciduous forests associated with the Atlantic Forest domain (Coelho et al., 2016, 2018). The species composition includes families with wide geographical distributions, although many species are largely endemic and reveal the former isolation of this refuge, which can be called a cloud forest. Compared with lowland forests, these forest islands have a lower canopy and a greater abundance of epiphytes, with a significant representation of Araceae, Orchidaceae, Bromeliaceae,

Pteridophyta, and Bryophyta. This elevated representativeness of epiphytes is a consequence of the high humidity in these formations (Whitmore, 1990; Van der Hammen, 1995; Webster, 1995). The plant families with the greatest species richness in these forest islands are Myrtaceae, Lauraceae, and Melastomataceae, followed by Fabaceae, Asteraceae, and Rubiaceae (Coelho et al., 2016). Parameters such as density, diameter, average height, richness and diversity of plant species vary conspicuously between the edge and the nuclear zones of the forest islands. The soil also differs spatially in its physicochemical characteristics and its conditions in nuclear zones are more favorable to the establishment of characteristic species of late stages of succession (Coelho et al., 2016). The climate is mesothermic (Cwb in the Köppen classification), with dry winters and rainy summers, a mean annual rainfall of 1500 mm and average annual temperature ranging from 17.4 to 19.8°C (Ferrari et al., 2016; Silveira et al., 2016).

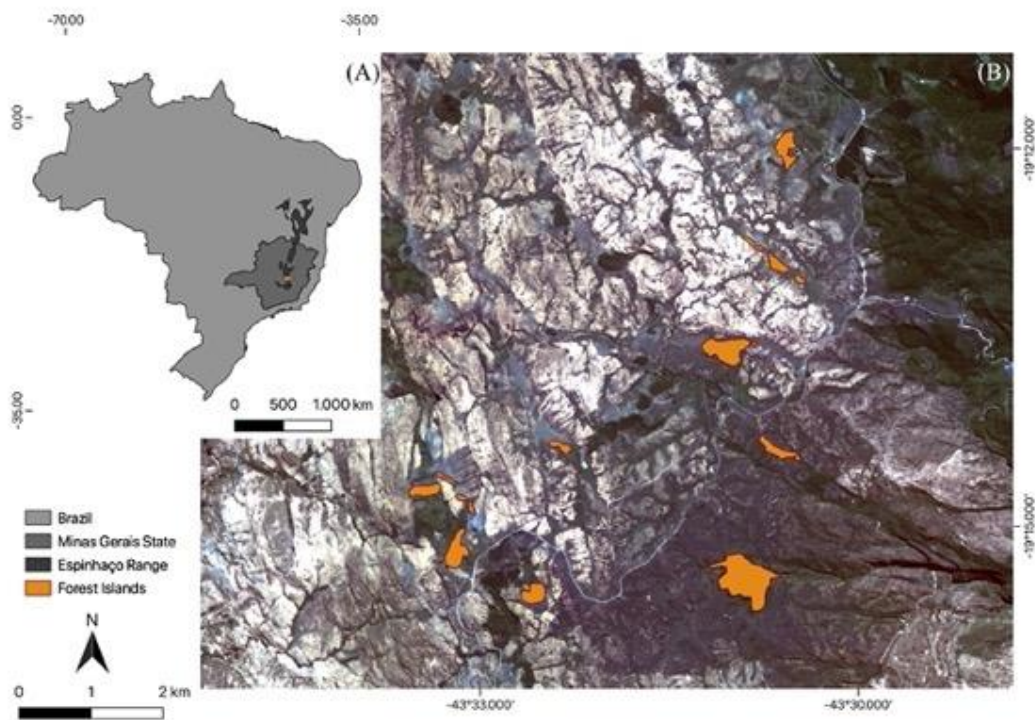


Figure 1. Map showing (A) Espinhaço Range in Brazil and (B) the 14 naturally-fragmented forest islands (orange shapes) where we sampled herbivorous insects in a *campo rupestre* matrix of the Serra do Cipó, southern portion of the Espinhaço Range Biosphere Reserve, Minas Gerais, Brazil.

2.2 Sampling design

A total of 14 forest islands were selected. The chosen areas vary in size (1.21–39.89 ha, mean = 8.21 ha, SD = 10.24 ha) and shape (from circular to elongated limits), and are

spaced at variable distances (0.1–1.5 km) (see supplementary table 1 for more details). A 20 × 50 m plot was established in the center of each forest patch, where sampling was performed over two consecutive years (2014–2015) with two sampling events in the summer – rainy season (February 9–16, 2014; February 21–28, 2015) and two in the winter – dry season (August 16–23, 2014; August 22–29, 2015). In each sampling period we collected herbivorous insects using two Malaise traps (one soil Malaise trap and one canopy Malaise Window trap – mean height 4,5m ±SE 0,44 – see supplementary table 1 to check the heights of each Malaise window traps) located in the center of each plot, which remained in the field for seven days (9408 trap-hours for each type) (Perillo et al., 2020). These types of traps are one of the most widely used non attractant, static insect traps in surveys of insect diversity (Muirhead-Thomson 1991; Noyes, 1989; Southwood and Henderson, 2000; also see Skvarla et al., 2021 for a review). Collected herbivorous insects were grouped into one of three guilds according to their feeding habits: fluid-feeding, leaf-chewing or xylophagous insects (wood-associated fauna) (Macedo-Reis et al., 2019). We considered as herbivorous insects every insect belonging to families that directly or indirectly depend on plant resources for survival (Moran and Southwood, 1982; Neves et al., 2014; Macedo-Reis et al., 2019). The insects were identified using taxonomic keys and separated into morphospecies based on external morphological features. All collected insects were stored in the entomological collection of the Laboratory of Insect Ecology at the Federal University of Minas Gerais (Universidade Federal de Minas Gerais - UFMG).

2.3 Herbivorous insect guilds

We chose to work with exophagous insects, which are free-living organisms that move within and between plant species in search of resources. They present different life-forms (Neves et al., 2010; Araújo, 2013) and can be classified into several trophic guilds according to their feeding habit (Novotny et al., 2010), such as fluid-feeding herbivores, with a modified oral apparatus or stylet to suck plant sap (Ribeiro et al., 1994); chewing herbivores, with well-developed jaws specialized in cutting and grinding plant tissue (Raupp, 1985); and xylophagous herbivores, that breed in inner bark (dead phloem tissue; Raffa et al., 2015) and some feed on symbiotic “ambrosia” fungi that grow in the nutrient poor xylem tissue of woody plants (Gohli et al., 2017). In the case of fluid-feeding

herbivores, the stylet needs to overcome the physical protective barriers of plants, such as waxes and trichomes, to access plant tissues. Thus, they are mostly affected by sap nutrient content (Price, 1997; Huberty and Denno, 2006) and tend to specialize more than chewing and xylophagous herbivores by surviving for several generations on a single host plant (Denno and Perfect, 1994; Ødegaard, 2003; Novotný et al., 2010). Chewing herbivores generally have a broad diet of host plant species and are directly influenced by leaf mechanical properties and chemistry (Peeters, 2002; Read and Sanson, 2003). They are considered to comprise the most abundant and species-rich guild (Novotny et al., 2012). Xylophagous herbivores feed on several host families with generally low host specificity (Beaver, 1979; Macedo-Reis et al., 2016) and many of them are capable of quick dispersal and establishment in new habitats (Allen and Humble 2002, Haack 2006). The perception of landscape structure by all these insect guilds in different habitats depends on their dispersal ability and foraging range (da Silva et al., 2019; Toivonen et al., 2017; Weibull et al., 2000), which differ among guilds due to several factors, including habitat selection and mortality risks, potentially influencing them to move within forest environments (Tews et al., 2004; Macedo-Reis et al., 2019). Also, these herbivorous insect feeding guilds may respond differently to the same habitat conditions due to their level of specialization and life history constraints (Denno & Roderick 1991, Vehviläinen et al. 2007, Sobek et al. 2009). Thus, different feeding guilds respond to environmental characteristics differently, especially if we consider different spatial scales (Neves et al., 2013; Lourenço et al., 2015).

2.4 Data analysis

In order to show extrapolated values of species richness to a similar number of individuals we constructed rarefaction curves using the R package ‘iNEXT’ (Chao et al., 2014; Hsieh et al., 2016), available at <https://chao.shinyapps.io/iNEXTOnline/>. We accounted for every individual collected in the two Malaise traps, in all different seasons, for the three guilds of herbivorous insects. Thus, we estimated the sample completeness for each individual sampled. For extrapolation curves, the number of individuals was up to twice the actual reference size (Chao et al., 2013). We then built rarefaction curves with different sampling intensities, these curves representing the gamma diversity of each stratum per herbivorous insect guild. The sample units (i.e., the 14 forest islands) were

used as the independent variable and the richness of each herbivorous insect guild was the dependent variable. Thus, we were able to obtain information about the completeness of herbivorous insect species in relation to each sampling unit. We also assessed the alpha diversity in our smallest sampling unit for each herbivorous insect guild. For this, we used the hill number ^0D to show the observed accumulated species richness for our sampling units, with their respective confidence intervals. The non-overlapping of confidence intervals indicates that the insect richness found in the canopy is lower for all three guilds.

To test our hypothesis that spatial scale has a main contribution to the total diversity of herbivorous insects, we partitioned the γ -diversity (i.e. diversity in the 14 islands) into α -diversity (i.e. diversity within Malaise traps) and β -diversity (which was partitioned into β_1 – between strata within forest sites; β_2 – among forest islands within sampling dates and β_3 – over sampling dates). We performed these analyses with the ‘adipart’ (additive diversity partitioning) function, which works with a statistic returned by a function that is assessed according to a nested hierarchical sampling design (our three dimensions), both from the R package ‘vegan’ (Oksanen et al., 2018). We used this function only to describe the species richness per dimension.

We assessed the spatial and temporal variations of the herbivorous species composition (β -diversity) using the Sørensen dissimilarity index in a multiple-spatial and time approach (see Baselga, 2010; Neves et al., 2021). So, we decomposed total spatial and temporal β -diversity among the forest islands (using the Sørensen and Simpson index of similarity), which we partitioned into turnover and nestedness-related components using the ‘beta.multi’ function in the ‘betapart’ R package (Baselga and Orme, 2012). Data were aggregated by forest sites for the spatial partition of β -diversity among sites and aggregated by sampling dates for the partition of β -diversity over sampling dates. The function ‘beta-multi’ includes the functions to compute multiple-site dissimilarities β_{SOR} , β_{SIM} and β_{NES} , called beta.SOR(x), beta.SIM(x) and beta.NES(x), respectively, where x is a data frame in which sites are rows and species are columns. We used the results of this calculation to determine whether species substitution or species loss/gain influenced the general spatial pattern of temporal β -diversity (Baselga, 2010; Neves et al., 2021).

Linear mixed models (LMMs) were used to test the effect of the strata on each herbivore guild (fluid-feeding, leaf-chewing and xylophagous) temporal β -diversity over seasonal samples, where temporal β -diversity was used as a dependent variable and the

strata as an independent variable. The identity of each forest island (14 in total) was used as a random factor in LMMs, to account for spatial pseudoreplication (Bolker et al., 2009). The lme4 package and lmer function were used to perform LMM analyses (Bates et al., 2018). The function Anova of package car, which allows ANOVA in mixed models, was used to deem variables significant or not. All models were subjected to residual analyses to check for model fit and error structure suitability (Crawley, 2013). All statistical analyses were performed using R software v.4.0.

3 Results

3.1 General patterns

We recorded a total of 6597 herbivorous insects belonging to 41 families, two subfamilies and 557 morphospecies (Table 1). Among these morphospecies, 290 were fluid-feeding, 147 were leaf-chewing and 120 were xylophagous insects. Among fluid-feeding herbivorous insects, Cicadellidae and Psyllidae were the richest in species (28%) and most abundant (72.9%), with the Cicadellidae family alone representing 22.1% and 69.7% of the total richness and abundance, respectively. For leaf-chewing insects, Chrysomelidae and Curculionidae were the richest in species (23.5%) and most abundant (13.4%) while for xylophagous insects, Cerambycidae and Scolytinae were the richest in species (9.7%) and Cerambycidae and Anobiidae were the most abundant (2.1%), together representing 61.2% of the total richness and 88.4% of the total individuals sampled. There was also a high number of rarely sampled species, comprising 244 singletons (43.8% of the total) and 84 doubletons (15.1% of the total). Of these, 120 singletons and 38 doubletons belonged to fluid-feeding insects guild, 58 singletons and 26 doubletons belonged to leaf-chewing insects guild and 65 singletons and 20 doubletons belonged to xylophagous insects guild. In addition, we had a greater number of unique morphospecies collected in the understory for all guilds. A total of 398 (71.5%) morphospecies were collected exclusively in the understory (224 fluid-feeding insects; 115 leaf-chewing insects; 59 xylophagous insects), while 63 (11.3%) were collected exclusively in the canopy (18 fluid-feeding insects; eight leaf-chewing insects; 37 xylophagous insects) and 96 (17.2%) in both strata (48 fluid-feeding insects; 24 leaf-chewing insects; 24 xylophagous insects).

Table 1. Herbivorous insects morphospecies richness and abundance sampled in Serra do Cipó, Minas Gerais, Brazil.

Guild	Family	Total richness	Total abundance	Strata			
				Understory		Canopy	
				Abundance	Richness	Abundance	Richness
Fluid-feeding	Achilidae	28	150	145	28	5	2
	Aetalionidae	2	2	2	2	0	0
	Aphididae	2	3	2	2	1	1
	Aphrophoridae	2	2	2	2	0	0
	Berytidae	1	4	4	1	0	0
	Cercopidae	7	10	9	7	1	1
	Cicadellidae	123	4601	4349	113	252	41
	Cixiidae	11	15	15	11	0	0
	Cydnidae	1	8	8	1	0	0
	Delphacidae	6	10	10	6	0	0
	Derbidae	3	99	98	3	1	1
	Flatidae	1	1	1	1	0	0
	Fulgoridae	1	3	3	1	0	0
	Issidae	2	5	5	2	0	0
	Kinaridae	1	1	1	1	0	0
	Largidae	1	1	1	1	0	0
	Lygaeidae	10	77	74	10	3	3
	Membracidae	16	33	32	15	1	1
	Miridae	21	81	70	20	11	3
	Pentatomidae	4	4	4	4	0	0
	Psyllidae	33	210	183	27	27	12
	Pyrrhocoridae	1	1	1	1	0	0
	Rhopalidae	3	4	3	3	1	1
	Thyreocoridae	1	1	1	1	0	0
	Tingidae	9	20	20	9	0	0
Leaf-chewing	Anostomatidae	2	2	2	2	0	0
	Attelabidae	1	4	4	1	0	0
	Chrysomelidae	69	688	639	67	49	18
	Curculionidae	62	196	181	57	15	13
	Erotylidae	6	9	9	6	0	0
	Gryllidae	3	17	17	3	0	0
	Megalopodidae	1	1	1	1	0	0
	Meloidae	1	1	1	1	0	0
	Tettigoniidae	2	2	1	1	1	1

continues on the next page

Table 1. Herbivorous insects morphospecies richness and abundance sampled in Serra do Cipó, Minas Gerais, Brazil.

Guild	Family	Total richness	Total abundance	Strata			
				Understory		Canopy	
				Abundance	Richness	Abundance	Richness
Xylophagous	Anobiidae	21	67	35	17	32	14
	Anthribidae	18	30	26	17	4	3
	Bostrichidae	5	19	3	3	16	2
	Brentidae	7	21	19	7	2	1
	Buprestidae	4	14	14	4	0	0
	Cerambycidae	27	72	58	23	14	8
	Cupedidae	4	4	0	0	4	4
	Platypodinae	7	42	30	4	12	7
	Scolytinae	27	62	12	8	50	22

The sampling effort was sufficient to characterize the insect community sampled, with the rarefaction-extrapolation accumulation curves presenting a greater sampling coverage for those carried out in the understory (Fig. S1), where the observed and extrapolated guilds richness and abundance was higher. The greatest sampling was found for fluid-feeding insects, followed by leaf-chewing insects and xylophagous insects. We observed that the fluid-feeding species richness ranged between 66 and 272 species and its total abundance ranged between 303 and 5043, which corresponds to 87% and 97% of the sampling coverage values, and 91% and 99% of the extrapolated sampling coverage abundance along the canopy and the understory, respectively (extrapolated sample coverage richness = 99 and 357 along the canopy and the understory, respectively). For the leaf-chewing insects, we observed species richness ranging between 32 and 139 species and its total abundance ranged between 65 and 855, which corresponds to 68% and 93% of the sampling coverage values, and 85% and 97% of the extrapolated sampling coverage abundance along the canopy and the understory, respectively (extrapolated sample coverage richness = 46 and 176 along the canopy and the understory, respectively). Finally, we observed that xylophagous species richness ranged between 61 and 83 species and its total abundance ranged between 134 and 197, which corresponds to 74% and 72% of the sampling coverage values, and 86% and 80% of the extrapolated sampling coverage abundance along the canopy and the understory, respectively (extrapolated sample coverage richness = 87 and 129 along the canopy and the

understory, respectively). We also found that the diversity of the herbivorous insects sampled in this study was higher in the understory for all three guilds for both observed and extrapolated values (Fig. 2).

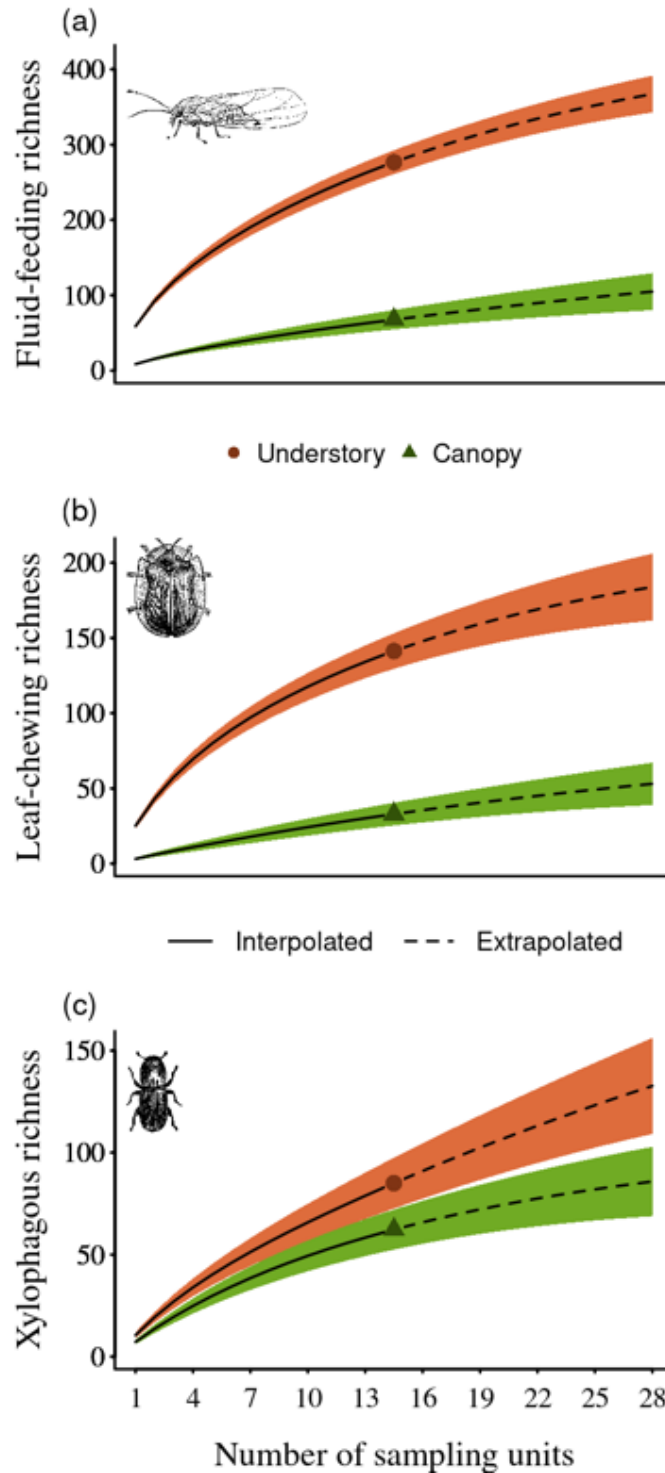


Figure 2. Species diversity curves (^0D) for samples (solid lines) and extrapolated samples (dashed lines) as a function of sample size according to the count of incidences of a) fluid feeding herbivores, b) leaf chewing herbivores and c) xylophagous herbivores in each sampling unit (i.e. forest island). The bar error represents the 95 confidence interval. The red circles in the red line represent the observed samples for understory and the green triangle for the canopy, obtained by a bootstrap method based on 1000 iterations.

3.2 Partition of diversity

We observed a main contribution of temporal scale (β_3) to the total diversity when partitioning the total insect species richness for each guild into its additive components (i.e. within Malaise traps (α), between strata within forest sites (β_1), among forest islands within sampling dates (β_2), and over sampling dates (β_3)) (Fig. 3). On the other hand, we found a smaller contribution of spatial scale between strata (β_1) to the total diversity for each insect guild. The observed β_3 over sampling dates was slightly greater for xylophagous insects (86.49%) than for fluid-feeding (79.90%) and leaf-chewing insects (83.43%). In contrast, the contribution of α , β_1 and β_2 was, respectively, only 7.45%, 5.17% and 7.48% for fluid-feeding insects, 6.19%, 3.38% and 7% for leaf-chewing insects and 3.95%, 3.25% and 6.31% for xylophagous insects. When we decomposed spatial and temporal β -diversity into its turnover and nestedness components, we verified that it was mostly represented by the turnover (β_{SIM}) component in all cases. This component explained more than 75% of the total β -diversity for all guilds and strata (Table 2).

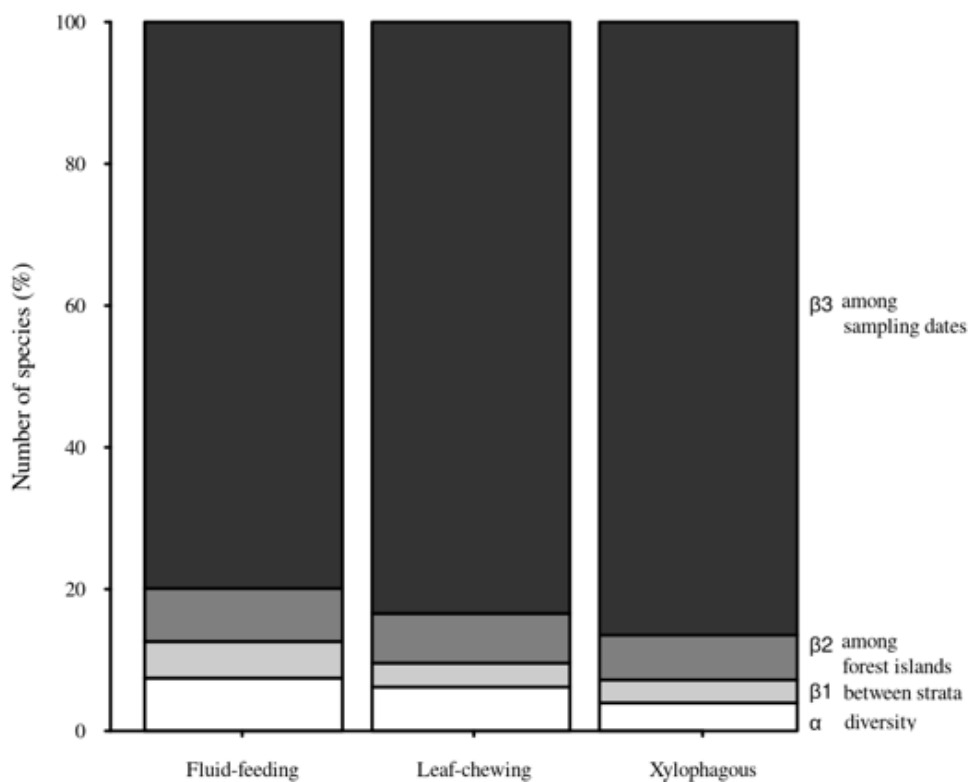


Figure 3. Contribution of the diversity of Malaise traps (α), between strata within forest sites (β_1), among forest islands within sampling dates (β_2) and over sampling dates (β_3) to the total diversity (γ) of herbivorous insects sampled in Serra do Cipó, Minas Gerais, Brazil

Table 2. β -Diversity using the Sørensen index for herbivorous insects collected in both strata and the importance (%) of turnover (β_{SIM}/β_{SOR}) for each guild at each stratum.

Stratum	Guild	Spatial β -diversity	Turnover (%)	Temporal β -diversity	Turnover (%)
Understory	Fluid-feeding	0.85	0.96	0.62	0.94
	Leaf-chewing	0.89	0.97	0.65	0.79
	Xylophagous	0.93	0.96	0.82	0.91
Canopy	Fluid-feeding	0.92	0.97	0.80	0.93
	Leaf-chewing	0.95	0.97	0.88	0.92
	Xylophagous	0.94	0.96	0.90	0.90

The species composition over time (Temporal β -diversity/ β_{SOR}) varied between vegetation strata for fluid-feeding ($F = 54.12$; $Df = 1$; $p < 0.001$) and leaf-chewing insects ($F = 20.16$; $Df = 1$; $p < 0.001$), with higher values for the canopy (Fig. 4). Temporal β -diversity of the xylophagous insects did not show variation between strata ($F = 1.27$; $Df = 1$; $p = 0.27$).

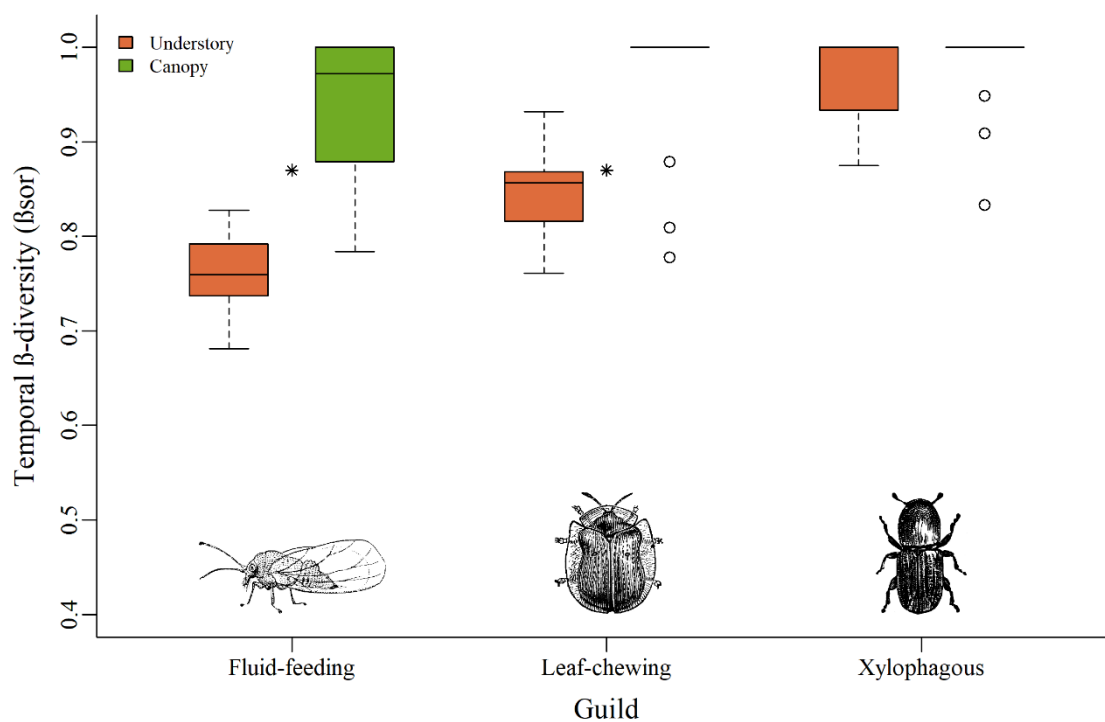


Figure 4. Boxplots of temporal β -diversity relating each forest island to the sampled stratum, for all three guilds of herbivorous insects. Bars represent the interquartile range with the median value. Circles indicate outliers. Stars reflect temporal β -diversity of the two insect guilds that showed relation with the stratum. Dashed lines indicate minimum and maximum values.

4 Discussion

In this study, we evaluated the influence that different spatiotemporal scales have on three free-feeding herbivorous insect guilds (fluid-feeding, chewing and xylophagous insects) in montane forest islands immersed in a grassland-dominated matrix (*campo rupestre*). We highlight a main contribution of time scale in the organization of the herbivorous insect community, mainly by turnover, with small differences among guilds. We could see the role of seasonality determining the local variation of species composition, corroborating that we have a highly variable always-green system over space and time, where the understory community varies less compared to the canopy community.

Among the several approaches that have been proposed to study patterns and processes that rule insect diversity across fragmented habitats, spatial metrics, such as patch (e.g., canopy cover, distance to continuous forest) and landscape attributes (e.g., percentage of forest in the landscape, number of patches, patch shape complexity) have been acknowledged to affect diversity patterns and distribution of several groups of insects in mountainous forest islands (da Silva et al., 2019; Perillo et al., 2020). Additionally, studies on temporal issues have drawn attention to help us understand and explain biodiversity dynamics in terrestrial fragmented habitats. Here, we found that the temporal scale exceeded the spatial scale in explaining herbivorous insect diversity, which is the opposite of what was expected for our first hypothesis. Most studies have found a higher predictive power of spatial scale than temporal ones over insect community structure in tropical ecosystems (da Silva et al., 2019; Castro et al., 2020). However, we found a higher importance of seasonal variation on the composition of all three insect guilds sampled in this study. These results indicate that, more than patch attributes, factors such as seasonal variation in temperature and humidity are drivers to temporal variation in resources that directly affect herbivorous insects that inhabit these forest islands. Thus, despite being an evergreen forest, the climatic seasonality of these forest islands is the most important driver for all herbivorous insect guilds sampled in this study and contribute more to their diversity and differences in species composition than spatial factors such as the distance among the forest islands or the vertical stratification (see Macedo-Reis et al., 2016; Novais et al., 2018).

We also found that the vertical stratum was an important factor driving the composition of fluid-feeding and leaf-chewing insect guilds, partially corroborating our

third hypothesis. Similarly to our findings, wasps and bees (Perillo et al., 2020) and dung-beetles (da Silva et al., 2019) also have high temporal β -diversity (β_{sor}) in this study system, indicating that the composition of insect communities varies greatly throughout seasons. In fact, all three herbivorous insect guilds, regardless of the strata, showed high temporal β -diversity, corroborating that we do have a highly variable system over space and time. However, fluid-feeding and leaf-chewing insects presented a greater temporal β -diversity for the canopy, which is the opposite of the pattern found for ants in a tropical dry-forest (Neves et al., 2021). The temporal β -diversity of both fluid-feeding and chewing insects being higher in the canopy than in the understory may be linked to the different effects of seasonality on specific microhabitats of these two strata. However, it may also be related to the insect diversity sampled in the understory that was much higher than that sampled in the canopy (which harbors more rare species and therefore has less redundancy) (see Skvarla et al., 2021). Besides, it is important to note that the insect guilds can respond differently to seasonal changes in resource availability between canopy and understory (see also Neves et al., 2014; Macedo-Reis et al., 2019).

Tropical forests have a vertical gradient of microclimatic conditions from the ground level to the canopy, with an increase of temperature and solar radiation, and a decrease in air humidity (Law et al., 2019). In this way, for herbivorous insects associated with forest islands system, it would be reasonable to think that the canopy has more unstable characteristics than the understory. For example, the increase in temperature and solar incidence is directly related to the survival of beetles from the Chrysomelidae and Curculionidae families, since it represents one of the main mortality factors of these insects (Lill and Marquis, 2007). In addition, the greater solar radiation can cause adult individuals of the Cicadellidae family to disperse less or to seek more humid and shaded areas (Ott and Carvalho, 2001; but also see Lessio and Alma, 2004). However, the canopy also has greater turnover of leaves and flowers (Basset et al., 2003a), resources that are especially important for fluid-feeding and chewing insects (Basset et al., 2003b). In this regard, it is known that the life cycle of individuals from the Cicadellidae and Psyllidae family probably follows the phenological pattern of leaf exchange in plants (Novais et al., 2018). Thus, we can expect that an environment with more changes in its conditions that presents, at the same time, more and better resource availability for its associated insects, will present greater temporal β -diversity for fluid-feeding and chewing insects. The same could not be observed for the guild of xylophagous insects, which is similar to

the pattern reported among Scolytinae in Malaysian forests (Simon et al., 2003). This pattern could be explained by their close association with the range of suitable wood availability (Grove, 2002; Hulcr et al., 2008), and not leaves. Therefore, wood diameter and air moisture content seem to be better predictors of their diversity (Macedo-Reis et al., 2016), since they feed and spend much of their lives inside the bark, with little interaction with the external environment (Wood, 1982; Zuo et al., 2016). Here, it is important to emphasize that although Lepidoptera like the Symphita larvae are very important representatives of chewing herbivorous insect guild, they were not considered in our results especially due to the limitations of sampling traps (see Schmidt, 2016; Rosa et al., 2019; Skvarla et al., 2021).

When we consider the β -diversity decomposition into turnover and nestedness, we found species turnover as the main driver of β -diversities for the three herbivorous insect guilds in all spatio-temporal scales. This high species replacement supported our second hypothesis and has been documented in similar environments as the most important component of dissimilarity in species over time (Oliver et al., 2016; Nunes et al., 2020; Neves et al., 2021). A greater species turnover implies in high substitution of species, which indicates that each forest island must have a unique community. From this perspective, forest islands can be considered transient environments with great conservation value for many species (Vieira et al., 2008), where their presence can be considered a sample of the dispersers coming from continuous forest and even from open surrounding areas, which, in part, can explain the high rates of rare species (43.8% singletons and 15.1% doubletons) sampled in this study. Similar rates of rare species have been commonly observed in tropical arthropod studies (Coddington et al., 2009), and especially in high-elevation tropical mountains (Perillo et al., 2017). Thus, we argue that species turnover is an important factor for maintaining high diversity in forest islands in tropical mountain areas. Besides, it is important to notice that this system must be linked to metacommunity structure. Preliminary data from a long-term research project (Long term ecological research from *campo rupestre* – CRSC) also points out to the existence of a dynamic of insect metacommunities among forest islands, where both local (size, shape) and landscape (degree of isolation) characteristics can jointly influence the spatiotemporal dynamics of the structure of metacommunities that inhabit this ecosystem. For example, recent studies carried out with different insect taxa, including ants (Brant et al., 2021), dung beetles (Da Silva et al., 2019), fruit-feeding butterflies (Pereira et al.,

2017), and wasps and bees (Perillo et al., 2020), have found high species turnover rates among forest islands, showing the importance of each forest island in maintaining the structure and conserving the communities associated with the entire archipelago. Despite the small distance among the forest islands, this provides a valid explanation of spatial and temporal dynamics, driven by habitat heterogeneity and environmental filters, with forest fragments connected by dispersal among habitats.

We presented a diverse array of spatiotemporal distributions among herbivorous insect guilds. Both spatial and temporal factors have mixed contributions in shaping the observed patterns, and the main differences among guilds reflect their use of resources. We showed that in altimontane forest systems there is a great change in the composition of herbivorous insects that are especially shaped by temporal variations in climatic characteristics. Besides, our findings suggest that there are differences between strata, where the understory of this studied system is more diverse and stable than the canopy. Since the montane forest islands are located at a higher elevation with a great propensity to be affected by global changes (Nunes et al., 2020), we suggest that long-term ecological research on herbivorous community structure in relation to climatic variation is a key element for future investigations, which can be decisive for the conservation of herbivorous insect communities. Beyond that, it can work as an advantageous strategy for the development of environmental conservation and monitoring programs, as long-term studies that include multiple sites within a regional species pool enable a thorough assessment of biodiversity change. Additionally, the effects of anthropogenic pressures, such as fire and the constant presence of cattle around this complex forest archipelago system, must be monitored (see Coelho et al., 2018) if we expect to manage and conserve biological diversity in a sustainable manner, since these forest islands may serve as warming refuges in a fragmented landscape holding an invaluable diversity of species that, without these old-growth forest reservoirs, would be doomed to disappear (see Janzen and Hallwachs, 2019). In a changing world, supporting and maintaining monitoring efforts in these systems, including other regions of the Espinhaço Range, will certainly bring an advance in knowledge and will be very useful for our current understanding of the effects of anthropogenic pressures and climate change on communities that are associated to naturally insular systems.

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Supplementary material

Supplementary table 1. An overview of each sampled forest island, where PERIM refers to the Perimeter; NFI is the distance from the nearest forest island measured from the center point of each island, which is the location of the malaise traps; and MWH is the height at which each malaise window trap was installed.

Forest islands	Altitude (m)	Landscape Metrics			Total diversity of insects sampled		MWH (m)
		AREA (m ²)	PERIM (m)	NFI (m)	Total richness	Total abundance	
1	1239	12938	480	379	82	311	6,35
2	1262	43081	1008	331	91	388	8,15
3	1234	16316	857	331	94	394	8,7
4	1269	169562	2836	1270	110	747	6,5
5	1309	29715	911	1530	123	442	3
6	1317	113398	2219	575	110	313	15,8
7	1331	58653	1191	200	118	418	8,7
8	1271	69033,93	1548,00	1416	89	212	3,5
9	1230	398900,00	3726,00	1864	102	390	5
10	1324	92131,79	2070,00	1255	98	833	6,2
11	1273	12515,13	640,60	264	82	226	6,85
12	1267	12130,40	526,50	264	130	678	10,7
13	1290	25039,89	1230,00	200	96	366	7,9
14	1235	95738,92	2162,00	1590	161	879	5,5

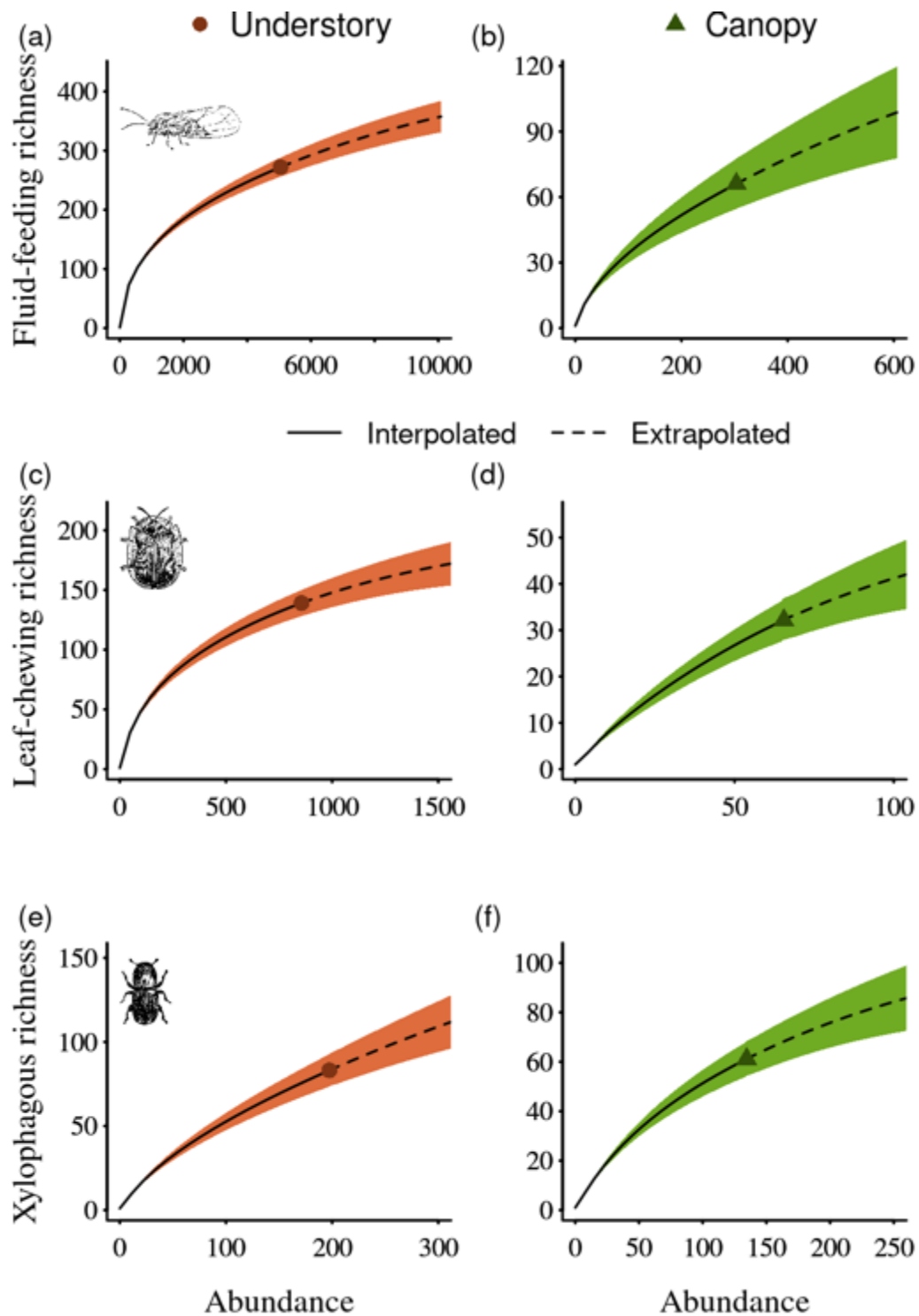


Fig. S1. Rarefaction-extrapolation species accumulation curves of herbivorous insects richness and abundance along the strata: observed and extrapolated richness and abundance values for (a) fluid-feeding insects sampled in the understory; (b) fluid-feeding insects sampled in the canopy; (c) leaf-chewing insects sampled in the understory; (d) leaf-chewing insects sampled in the canopy; (e) xylophagous insects sampled in the understory; (f) xylophagous insects sampled in the canopy.

CHAPTER 2

Interaction between cattle and fire shapes vegetation dynamics in a tropical forest-grassland mosaic



Juliana Kuchenbecker, Flávio Camarota, Ricardo Solar, Diego R. Macedo, Geraldo W.

Fernandes, Luiz Eduardo Macedo-Reis; Frederico S. Neves

Keywords: anthropic disturbances; Atlantic Forest; campo rupestre; forest islands; natural fragments; tropical mountains

Abstract

Forest-grassland mosaics represent alternative biome states and are a key feature of many natural communities across the Earth. However, understanding and managing these mosaics is complex due to the intrinsic ecological differences of each ecosystem, which

usually responds differently to disturbances such as fire and cattle grazing. We investigated how fire and cattle grazing drive canopy cover variation and landscape properties in natural forest islands immersed in a grassland matrix of a megadiverse mountain by monitoring 14 forest islands of different sizes and shapes. We predicted that both fire and cattle presence decrease the canopy cover over time, leading to large spatiotemporal variation of landscape metrics. We found that fire increased canopy cover variation, especially under cattle absence, probably because of the creation of firebreaks through trampling. Notwithstanding, the variation in area and perimeter of the forest islands was correlated neither with fire nor cattle presence. Our results emphasize fire as a major threat to this system, indicating a potential benefit of large grazers in protecting these fire-sensitive forest islands. Additionally, our results suggest that cattle grazing can partially offset fire spread and severity, which have implications for management of tropical forest-grassland mosaics in mountains and elsewhere.

1 Introduction

The existence of alternative stable states under similar climatic conditions, such as closed-forests and open biomes, is a key feature of many natural communities across the Earth (Dantas et al., 2016; Pausas and Bond, 2021). Indeed, forest-grassland mosaics comprise a major component of tropical landscapes (Dinerstein et al., 2017). These megadiverse regions are home to large and unique biodiversity, and provide key ecosystem services to hundreds of millions of people worldwide, such as water provision and climate control (Pinillos et al., 2009). However, because of intrinsic differences in the ecology of forests and open biomes (Bond, 2019), understanding, managing, and restoring forest-grassland mosaics is more complex compared to landscapes dominated by either ecosystem alone. Given this complexity, forest-grasslands transitions are particularly vulnerable to global change, since even small changes in their environmental drivers can lead to dramatic changes in their ecosystem structure and composition (Oliveras and Malhi, 2016).

Current evidence suggests that disturbance is a major factor driving and maintaining alternative biome states and tropical vegetation mosaics (Dantas et al., 2016). While vegetation structure and community composition in forests are harmed by disturbance (Feng et al., 2021), open biomes are often disturbance-maintained ecosystems, requiring recurrent fires and/or large herbivores for the persistence of shade-

intolerant species and avoidance of woody encroachment (Buisson et al., 2019). In forest-grassland mosaics, inappropriate disturbance regimes may harm either forests (e.g. increasing fire frequency; Flores et al., 2021), grasslands (fire exclusion policies; Durigan, 2020), or both. Therefore, a vital issue for decision-makers and park managers is to determine and implement the appropriate disturbance regime that can sustain biodiversity in both fire-tolerant grasslands and fire-sensitive forests at the landscape scale.

While the role of fire has been more frequently invoked as a major factor shaping alternative biome states in tropical vegetation mosaics (Pausas and Bond, 2020), the role of large herbivores in driving the distribution of tropical biomes has received less attention. Nevertheless, evidence suggests that both extinct and extant large mammal herbivores are key players in plant evolution and vegetation patterns (Baggio et al., 2021; Dantas and Pausas, 2022; Overbeck et al. 2022; Durigan et al., 2022). Large herbivores have the potential to directly influence grass cover and tree sapling survival and growth, and the interaction of their activity with fire can dictate which plant forms dominate the landscape (Oliveras and Malhi, 2016). Ultimately, large herbivores can compact the soil and destroy root systems, which can alter the water and nutrient cycles of plant communities, weakening the forest edges and reducing the size of forest patches (Tanentzap and Coomes, 2012; Villar et al., 2022). Therefore, integrating evidence on how fire and herbivory interact to determine vegetation structure and distribution is a major knowledge gap that needs to be addressed for better management, conservation, and restoration programs in tropical forest-grassland mosaics.

Considering forest-grassland mosaics, we must focus on those associated with mountaintops, especially in the tropics. These tropical mountaintops often are dominated by forest-grassland mosaics which not only harbor extremely rich biodiversity, but also act as indicators of human-induced changes (Perrigo et al., 2020). Additionally, forest-grassland mosaics in mountains are marked by contrasting edaphic conditions: typically nutritious soil sustain tropical forests, whereas extremely nutrient-impovertished soils, even poorer than typical lowland grasslands (Pinillos et al 2009), support a grassland matrix. Particularly, at the summit of the second-largest Neotropical mountain chain, the Espinhaço range, a unique ecosystem comprised of a natural forest archipelago, locally known as *Capões de Mata*, is patchily distributed on a matrix of open grassland (Silveira et al., 2016). This ecosystem contributes to the high diversity pattern of these tropical

mountaintops, and protects two main hydrographic basins (Callisto et al., 2019; Kuchenbecker et al., 2021). However, due to increasing threats such as intensive fires and cattle raising, the dynamics and balance of the *Capões de Mata* can be severely altered (Pereira et al., 2017; da Silva et al., 2019). Thus, strategies for the preservation and maintenance of these particular forest islands must be at the top priorities of conservation plans and policymakers.

Here, we aimed to determine how fire and cattle grazing drive variation in canopy cover and landscape properties in natural forest islands immersed in a matrix of megadiverse montane grasslands. Canopy cover is a suitable indicator of forest integrity, given that increasing canopy cover allows invasion by shade-intolerant invasive grasses that strongly shift species composition in forest communities (Flores et al., 2021). Based on current evidence on the disturbance ecology of forest-grassland mosaics (Bond, 2019; Buisson et al., 2019), we predict that (i) fire and cattle presence decrease the canopy cover of the *Capões de Mata* over time and (ii) lead to a large spatio-temporal variation of landscape metrics of these natural forest islands. We sampled canopy cover variation and landscape metrics across multiple years to provide a temporal mechanistic understanding of the dynamics of tropical forest-grassland mosaics.

2 Materials and Methods

2.1 Study area

This study was performed in a natural forest archipelago located in the summits of the Serra do Cipó, (above 1200 m asl) southeastern Brazil (19°14'19"S, 43°31'35"W; Fig. 1), a region known for its high biodiversity and endemism (Bitencourt and Rapini, 2013; Fernandes, 2016; Silveira et al., 2016; Miola et al., 2021). The climate of the study area is mesothermic (Cwb in the Köppen classification), with dry winters and rainy summers, a mean annual rainfall of 1500 mm and average annual temperature ranging from 17.4 to 19.8°C (data from a meteorological-station Onset HOBO U30 data logger, which was installed at 1300 m a.s.l. in the study region, but see also Alvares et al (2013)). The study area occurs at the ecotone of two biomes, the Cerrado (Neotropical savanna) to the west and the Atlantic Forest to the east. In the continuous grassland matrix - *campo rupestre*, forest islands called *Capões de Mata* - hereafter *Capões* - merge as natural patches of

vegetation from mountaintops, which are maintained by specific climate and soil parameters and are generally associated with headwaters and small streams (Coelho et al., 2016). This ecosystem is floristically similar to the seasonal semi-deciduous forests associated with the Atlantic Forest domain (Coelho et al., 2016, 2018a). Species composition includes families with wide geographical distributions, although many species are largely endemic suggesting an ancient isolation of this refuge.

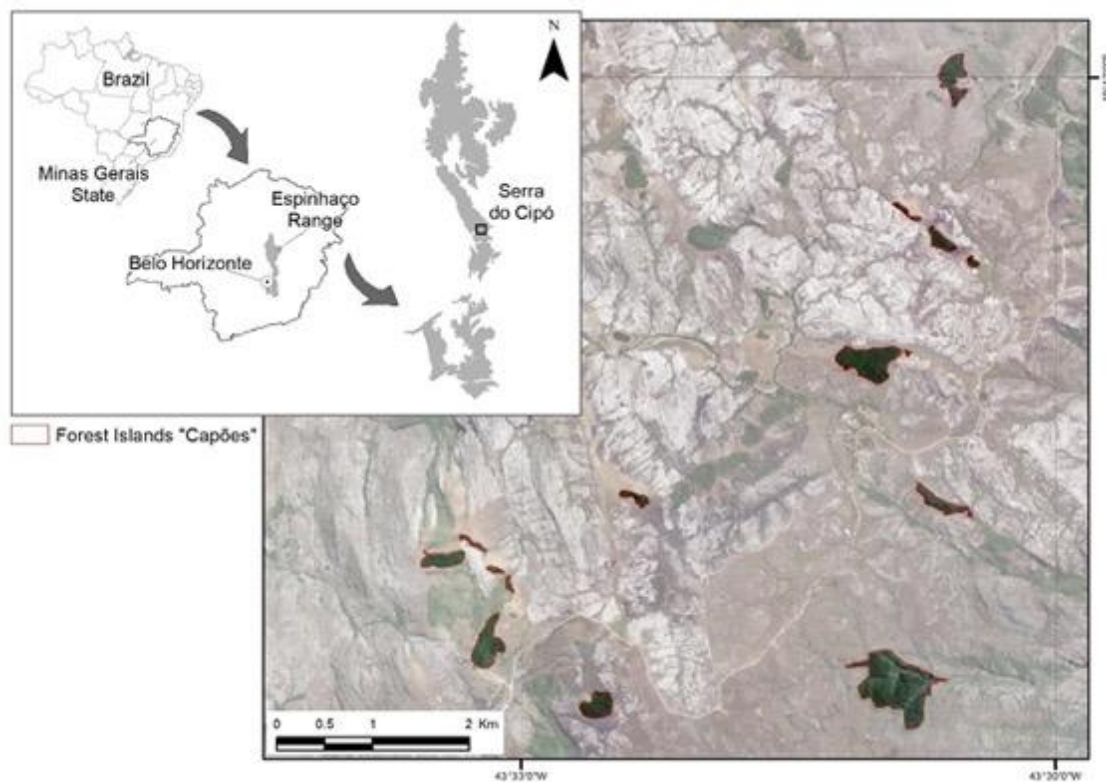


Figure. 1. Map of study area with location of the 14 montane forest islands (green) in a matrix of *campo rupestre* grassland (in gray) showed at Serra do Cipó, southeastern Brazil.

Compared with lowland forests, mountain forest islands have a lower canopy and a greater abundance of epiphytes, with a significant representation of Araceae, Orchidaceae, Bromeliaceae, ferns, and mosses. This elevated representativeness of epiphytes is a consequence of the high humidity in these formations (Whitmore, 1990; Van der Hammen, 1995; Webster, 1995). The richest tree families are Myrtaceae, Lauraceae, Melastomataceae, and Fabaceae (Coelho et al., 2018a). Soil physicochemistry, vegetation structure and composition vary conspicuously between the edge and the center of the *Capões*, with edges dominated by early-successional species.

(Coelho et al., 2016). Some *Capões* have gradually decreased in their area over successive dry seasons, due in part to frequent and intense fire events (Coelho et al., 2018b).

2.2 Sampling design

The sampled areas were established in the permanent plots of the Long-Term Ecological Research Project Campos Rupestres in 14 forest islands (i.e. 14 sample units). The chosen areas vary in size (1.21–39.89 ha, mean= 8.21 ha, SD= 10.24 ha) and shape (from circular to elongated limits), and are spaced at variable distances (0.1–1.5 km) from each other (see supplementary Table 1). A 20 × 50 m plot was established at the center of each forest island, where sampling was performed during the rainy season of 2014, 2015, 2018, and 2020. We took five 1.5 m height hemispherical photos with a fish-eye lens attached to a digital camera (Canon EOS Rebel T5i), one at each of the four plot vertices and one at the center of the plot. We also estimated the occurrence of fire and the presence of cattle in each plot, carrying detailed observations at the end of the dry season of each year (mid-October), based on the presence/absence of remains of recently burned vegetation and the presence of cattle feces. Thus, in a period of 48 hours within the period described above, we covered all the *Capões*, taking advantage of pre-existing trails made by cattle.

2.3 Data analyses

To evaluate the temporal variation of the canopy cover, the hemispherical photos taken were processed for the proportion between white and black pixels. Average values from the five photos (taken from the five points of each plot) were used to obtain a single canopy cover value for each forest island. The “ReadImages” (Oles et al., 2015) and “RT4Bio” (Reis Jr et al., 2015) packages were used to separate the white and black points of each photo and define the variation of the canopy coverage within the *Capões*. All photos were processed using R software v.4.0.

We used high resolution satellite images (< 1.0 m pixel size) through manual screen digitalizing to identify forest fragments in study area in 2014 and 2020. We calculated landscape metrics at patch level (Lausch et al., 2015) using Fragstats software (McGarigal, 1995). For each patch we measured area, perimeter, perimeter-area ratio, core area, and core area index (McGarigal, 2006) (supplementary Table 2). We then

calculated the delta of the landscape metrics by subtracting the values found for each measured metric per forest island in the year 2020 by the values found in the year 2014. This allowed us to determine temporal variation over time in the landscape metrics for each forest island.

We performed a Linear Model (LM) with the total canopy variation coefficient over the four samplings carried out in the seven years as a dependent variable, and the presence of cattle and the occurrence of fire, plus their interaction as independent variables. For that, each plot was qualitatively classified, with the presence or absence of fire and cattle. Linear Models (LMs) were also used to test the presence of cattle and occurrence of fire on landscape characteristics from 2014 to 2020, where landscape metric variation (Delta values) was used as a dependent variable and the interaction of presence of cattle and the occurrence of fire as an independent variable. All models were subjected to residual analyses to check for model fit and error structure suitability (Crawley, 2013). All statistical analyses were performed using R software v.4.0 (R Core Team, 2021).

3 Results

3.1 Presence of cattle and fire on forest island local-scale metrics

Of the 14 sampled forest islands, ten showed fire records, while cattle signs were recorded on eleven of them. Eight of the 14 sampled forest islands presented records of both fire and cattle grazing (Tab. 1). While the occurrence of fire increased the canopy variation, this variation was influenced by the cattle presence: burned forest islands in cattle absence showed the largest variation in canopy cover, and forest islands that had fire records and cattle presence showed lower variation in canopy cover (Tab. 2, Fig 2).

Table 1. Disturbance records and variation of forest islands landscape metrics from 2014 to 2020. AREA is Area patch; PERIM is Perimeter patch; PARA is Perimeter-Area Ratio which is equals the ratio of the patch perimeter (m) to area (m²); CORE is Core Area which is equals the area (m²) within the patch that is further than the specified depth-of-edge distance from the patch perimeter, divided by 10,000 (to convert to hectares); CAI is Core Area Index which is equals the percentage of a patch that is core area.

Forest Island	Disturbance records		Landscape metrics variation				
	Fire	Cattle	Δ AREA	Δ PERIM	Δ PARA	Δ CORE	Δ CAI
1	present	present	0	0	0	0	0
2	absent	present	0	0	0	0	0
3	present	present	0	0	0	0	0
4	absent	present	0	0	0	0	0
5	present	present	-6,21%	0	6,21%	-6,76%	-0,58%
6	present	present	-11,31%	12,35%	22,26%	-12,41%	-1,24%
7	present	present	0	0	0	0	0
8	present	absent	0	0	0	0	0
9	absent	absent	0	0	0	0	0
10	present	absent	-9,41%	0	9,41%	-9,74%	-0,36%
11	present	present	-7,53%	1,99%	9,37%	-8,85%	-1,43%
12	present	present	0	0	0	0	0
13	present	present	0	0	0	0	0
14	absent	present	0	0	0	0	0

Table 2. Linear Models showing the effects of the independent variables (presence of cattle, fire and their interaction) on the variation of canopy cover and landscape metrics over the seven years of sampling.

Dependent variables	Independent variables	Df	F value	Pr(>F)
Δ AREA	Presence of cattle	1	0.1697	0.6890
	Occurrence of fire	1	0.9389	0.3554
	Fire x cattle interaction	1	0.1012	0.7569
Δ PERIM	Presence of cattle	1	0.2444	0.6318
	Occurrence of fire	1	0.3275	0.5797
	Fire x cattle interaction	1	0.1001	0.7582
Δ PARA	Presence of cattle	1	0.2094	0.6570
	Occurrence of fire	1	1.3462	0.2729
	Fire x cattle interaction	1	0.0724	0.7933
Δ CORE	Presence of cattle	1	0.1347	0.7213
	Occurrence of fire	1	0.9058	0.3637
	Fire x cattle interaction	1	0.0822	0.7802
Δ CAI	Presence of cattle	1	0.2517	0.6267
	Occurrence of fire	1	1.3680	0.26933
	Fire x cattle interaction	1	0.0893	0.7711
Total Canopy Variation Coefficient	Presence of cattle	1	20.042	0.0012**
	Occurrence of fire	1	11.490	0.007**
	Fire x cattle interaction	1	17.086	0.002**

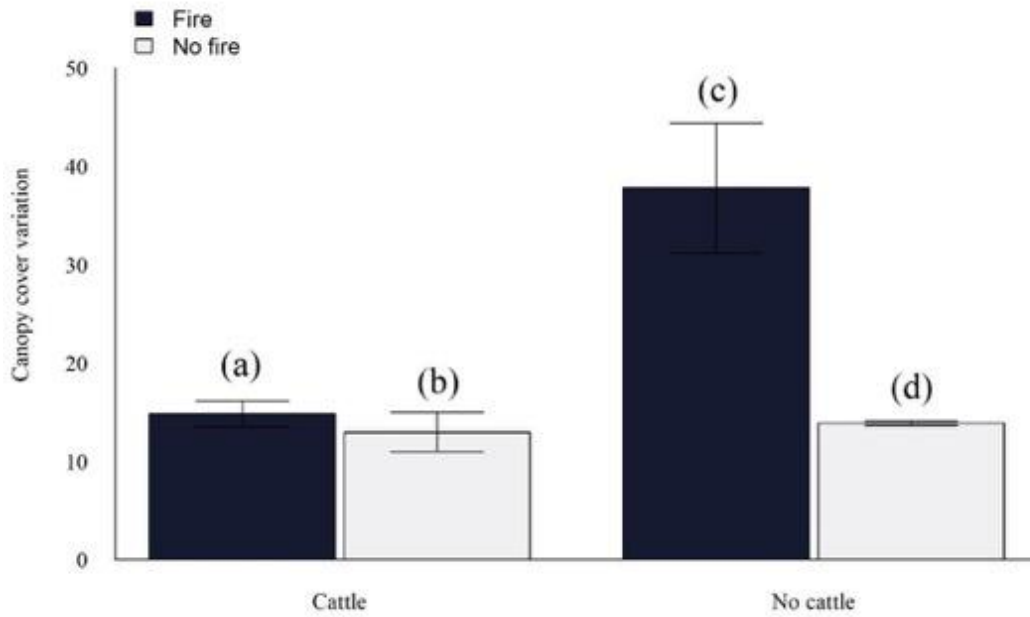


Figure 2. Effect of fire and cattle presence on canopy cover variation of forest islands at the Espinhaço Range, southeastern Brazil. Different letters represent significant differences among categories determined by linear models ($p < 0.05$).

3.2 General patterns and landscape-scale metrics

Few landscape metrics varied over time for some of the forest islands. From 2014 to 2020, four forest islands lost a small percentage of area, core area, and core area index. Similarly, the same four forest islands gained a small percentage of perimeter-area ratio. Additionally, out of these four, two increased their perimeter (Tab. 1). However, this variation in landscape metrics neither was correlated with fire nor the cattle presence (Tab. 2).

4 Discussion

Understanding how disturbance can be properly used for effective ecosystem management remains challenging in forest-grassland mosaics, but scientists and managers are increasingly becoming aware of the need to manage fire and large grazers to sustain biodiversity and ecosystem services (Baggio et al., 2021; Durigan et al., 2022). We found that the interaction between fire and cattle grazing shapes vegetation dynamics of natural islands of tropical rainforest in a megadiverse tropical forest-grassland mosaic, adding new evidence to the current debate on alternative biome states. As expected, fire

was found to be a major threat to forest islands, playing a strong role in canopy cover variation and stability of the system. Unexpectedly, however, this effect is drastically reduced by cattle presence, which can partially offset the adverse effects of fire. Finally, we also found that cattle grazing and fire had little effect on the observed temporal variation in landscape metrics.

Canopy cover variation was greater on forest islands under recurrent fire incidence. Canopy cover is the most widely used indicator of forest integrity (Chazdon et al., 2016), and a reliable predictor of vegetation dynamics in forest-grassland mosaics (Bond, 2019). In ecosystems with a closed canopy, severe fires can convert forests to open, shrub-dominated systems with denser, more continuous surface fuels that dry readily in the open conditions (Tepley et al., 2016). The post-fire vegetation is then more easily burned by subsequent fires (Paritsis et al., 2015; Tepley et al., 2016), and becomes more susceptible to invasive grasses (Flores et al., 2021). In this particular scenario, high-severity fires can reduce the tree canopy cover of a given fragment, resulting in dramatic and rapid understory plant community shifts, potentially accelerating the vegetation shifts expected with climate warming (Miller and Safford, 2020; Stevens et al., 2015). Thus, as a other evergreen, humid ecosystem (Coelho et al 2018b), *Capões* are threatened by perturbations in fire regimes (Keeley and Pausas, 2019).

We also found that cattle presence in the *Capões* indirectly reduces the effects of fire on canopy cover variation. Cattle activity in forests has been traditionally seen as detrimental, given its negative effects on tree regeneration (Blackhall et al., 2017). However, under low densities, cattle can actually benefit tree regeneration by reducing the biomass of grasses, and thus allowing tree saplings to grow above a fire-resistance threshold, increasing their above-ground densities (Oliveras and Malhi, 2016). Additionally, livestock herbivory can also reduce fire frequency and/or intensity through a reduction in fine fuel biomass and the creation of firebreaks during trampling (Davies et al., 2010; Evans et al., 2015). Our results indicate that cattle presence is not only associated with the consumption of palatable grasses, which decreases the amount of fine fuel, but also with the depletion of fine dead fuel associated with flammability when taking shelter or even bedding inside the forest islands. In addition, cattle presence can also decrease the vertical and horizontal distribution and continuity of the fine fuel, which supports its role as a natural firebreak for the system (see Celaya et al. 2022). This reduction in fine fuel may have reduced the chances of surface fire reaching the canopy

or spreading horizontally (Anderson, 1981; Flannigan et al., 2009). Despite our finding that cattle presence decreased canopy cover variation, it is important to consider that recent fire return intervals are way below their natural occurrence and, thus, likely influenced the cattle-mediated effects on canopy cover. Overall, our results are consistent with the interpretation that cattle grazing can partially offset fire spread and severity, especially on forest islands with high post-fire scrubland.

Cattle presence also decreased canopy cover variation in the absence of fire. Perhaps, this is a reminiscence of fire events prior to our sampling period (2014-2020), and therefore, the cattle are acting alone only on a relatively small timeframe. Moreover, these ecosystems were recently (~10kya) inhabited by a Megafauna consisting of large herbivores, which may have played a crucial role in shaping the present vegetation structure (Galetti et al., 2018; Dantas and Pausas, 2022). Therefore, to fully understand the dynamics of these forest-grassland mosaics, we must consider both recent and past disturbances (Pausas and Bond, 2020). Specifically, we need to take into account the potential role of large herbivores' density on their detrimental effects. The cattle density in the *Capões* is relatively small, with no more than 20 individuals at a given site (Kuchenbecker, personal observation). In comparison, in the open grasslands of southern South America, Bernardi et al. (2016) found that extremely high-density stocks maintained a relatively treeless ecosystem. Finally, cattle presence may also have negative effects not measured here, such as the destruction of headwaters. Therefore, a broader understanding of cattle effects on forest islands is important to better inform management strategies in complex forest-grassland mosaics.

The forest islands associated with the Espinhaço Range have a history of natural expansion and retraction mediated by edaphic properties and long-term climatic variation (Meguro et al., 1996 ab; Coelho et al., 2016). However, for edaphic grasslands (*sensu* Buisson et al., 2019), the extreme nutrient-impoverished soils of the *campo rupestre* grassland are thought to be a major factor restricting the forest expansion (Buisson et al., 2019). During the study period, we found variation in landscape metrics for some of the *Capões*, but variation was unrelated to cattle and fire presence. Therefore, although fire events play a fundamental role in controlling forest expansion (Hoffmann et al., 2003; Rossatto et al., 2009), our results provide evidence that the expansion and retraction of forest islands may be more related to natural processes than to be a consequence of land use and fire incidence. Nevertheless, this interpretation should be viewed with caution

since our study did not experimentally manipulate the drivers of vegetation expansion-contraction cycles.

5 Conclusions

Our results emphasize fire as a major threat to the *Capões de Mata* and highlight the complexity of the outcomes of disturbance by fire and large grazers, indicating a potential benefit of grazing in the protection of the fire-sensitive forest islands (Coelho et al., 2018b). To improve our knowledge, we must expand our sampling period and experimentally manipulate the presence of cattle and fire, which would gather crucial information regarding their effect. Since grazing effects in *campo rupestre* and its associated forest islands are largely unknown (Kolbek and Alves, 2008), we recommend caution in cattle grazing management in these environments, especially as we do not know yet to what extent this association is beneficial. We also draw attention to the need for the establishment of permanent plots dedicated to monitoring the long-term vegetation expansion and contraction of this forest-grassland mosaic to better track how global change-related drivers affect natural ecosystems (Magurran et al., 2010; Mirtl et al., 2018). Tropical and ancient mountains are a rich repository of biodiversity (Kumar and Sharma, 2017) and have the potential to improve our theoretical understanding of the historical and contemporary factors driving biodiversity distribution (McDougall et al., 2011; Guo et al., 2018), which is crucial for the long-term survival and well-being of people and nature.

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We especially thank Fernando A. O. Silveira for the invaluable discussion concerning the study system. We also thank Lucas Perillo for assistance with fieldwork. JK acknowledges a research scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES; 88887.288737/2018-00). RS and DRM thanks CNPq (305739/2019-0 and 309763-2020-7, respectively) for funding. FC, FAOS, GWF, and FSN thanks CNPq and FAPEMIG, and FC thanks CAPES for funding. Thanks also go to PELD-CRSC (APQ-03370-21), Reserva Vellozia, GSG and Parque Nacional da Serra do Cipó for logistical support.

Supplementary material

Supplementary table 1. An overview of each sampled forest island, where AREA refers to Area patch; PERIM refers to the Perimeter patch and NFI is the distance from the nearest forest island measured from the center point of each island.

Forest islands	Altitude (m)	Landscape Metrics year 2020		
		AREA (ha)	PERIM (m)	NFI (m)
1	1239	1,0972	522	379
2	1262	3,8453	1148	331
3	1234	1,5334	978	331
4	1269	16,5197	2668	1270
5	1309	2,4541	1006	1530
6	1317	9,1724	2300	575
7	1331	5,9051	1436	200
8	1271	6,3416	2104	1416
9	1230	37,6007	4182	1864
10	1324	6,564	1340	1255
11	1273	0,8314	604	264
12	1267	0,8527	508	264
13	1290	1,3759	970	200
14	1235	9,0769	2156	1590

Supplementary table 2. Landscape metrics of *Capões de Mata* in the years of 2014 and 2020. AREA refers to Area patch; PERIM refers to Perimeter patch; PARA is the Perimeter-Area Ratio which is equals the ratio of the patch perimeter (m) to area (m²); CORE refers to Core Area which is equals the area (m²) within the patch that is further than the specified depth-of-edge distance from the patch perimeter, divided by 10,000 (to convert to hectares); CAI is the Core Area Index which is equals the percentage of a patch that is core area.

Forest										
Islands	AREA_2014	AREA_2020	PERIM_2014	PERIM_2020	PARA_2014	PARA_2020	CORE_2014	CORE_2020	CAI_2014	CAI_2020
1	1,0972	1,0972	522	522	475,7565	475,7565	0,9809	0,9809	89,4003	89,4003
2	3,8453	3,8453	1148	1148	298,5463	298,5463	3,5903	3,5903	93,3685	93,3685
3	1,5334	1,5334	978	978	637,7984	637,7984	1,3211	1,3211	86,1549	86,1549
4	16,5197	16,5197	2668	2668	161,5041	161,5041	15,9143	15,9143	96,3353	96,3353
5	2,6166	2,4541	1006	1006	384,4684	409,9262	2,3868	2,2255	91,2176	90,685
6	10,3424	9,1724	2016	2300	194,9257	250,7523	9,8905	8,6626	95,6306	94,442
7	5,9051	5,9051	1436	1436	243,1796	243,1796	5,5634	5,5634	94,2135	94,2135
8	6,3416	6,3416	2104	2104	331,7775	331,7775	5,8798	5,8798	92,7179	92,7179
9	37,6007	37,6007	4182	4182	111,2213	111,2213	36,6301	36,6301	97,4187	97,4187
10	7,2457	6,564	1340	1340	184,9373	204,1438	6,9346	6,2595	95,7064	95,3611
11	0,8991	0,8314	592	604	658,4362	726,4854	0,7628	0,6953	84,8404	83,63
12	0,8527	0,8527	508	508	595,7547	595,7547	0,7363	0,7363	86,3492	86,3492
13	1,3759	1,3759	970	970	704,9931	704,9931	1,1697	1,1697	85,0134	85,0134
14	9,0769	9,0769	2156	2156	237,526	237,526	8,5978	8,5978	94,7218	94,7218

CHAPTER 3

Environmental and anthropic filters structure herbivorous insects communities in natural altimontane forest islands



Juliana Kuchenbecker, Flávio Camarota, Pedro Giovâni da Silva, Lucas Neves Perillo,
Luiz Eduardo Macedo-Reis; Frederico S. Neves

Keywords: *Campo rupestre*; canopy cover; cattle; community stability; Espinhaço Mountain Range; fire; forest-grassland mosaics; metacommunities

Abstract

Although herbivorous insects and their associated plants play a crucial role in the maintenance of the global terrestrial biodiversity, they are currently in decline worldwide mainly due to human-induced disturbances, which also threaten natural and important ecosystems. Here we asked whether the community stability of herbivorous insect species

is influenced by canopy cover variation and/or anthropic disturbances over time in a mountainous forest island archipelago. We checked if the stability of the herbivorous insect community differed between the vegetation strata and how canopy cover variation, the incidence of fire, and cattle presence affect this stability as well as colonization and extirpation processes. We conducted this study in natural forest islands immersed in a grassland matrix of a megadiverse mountain by monitoring 14 forest islands of different sizes and shapes, where we sampled 5567 herbivorous insects from 2014 to 2020. Fire was the only variable that influenced the stability of herbivorous insects and only the canopy cover variation explained the species' gains and losses. Moreover, the understory was more temporally stable than the canopy. The comprehension of dynamics underlying the stability of communities provides a robust way to predict how the organization of biodiversity and ecosystem functionality will change in response to further environmental changes, especially considering the major pressure of climate change on tropical altimontane forest systems. Conservation actions largely depend on a better understanding of temporal variation and new insights into ecological community structure across space and time of the organisms that inhabit them.

Introduction

The interactions between plants and herbivorous insects involve a relevant part of global terrestrial biodiversity (Price, 2002; Mora *et al.*, 2011; Stork & Habel, 2014), with these two megadiverse groups playing a major role in the maintenance of this diversity (Janzen, 1970; Connell, 1971; Marquis *et al.*, 2016). Nevertheless, most of this incredible diversity is currently in decline worldwide (Hallmann *et al.*, 2017; Wagner, 2020) due to a combination of climate change, habitat degradation, and land use change (Wagner, 2020). Among human-induced disturbances, cattle grazing and fire are increasingly disrupting plant and herbivorous insect interactions (Bond & Keeley, 2005). Indeed, these disturbances are often considered one of the largest threats to the dynamic of natural ecosystems, such as forest-grassland mosaics (Kuchenbecker *et al.*, *in press*). However, while these mosaics comprise a large diversity of plant and herbivorous insect interactions (Neves *et al.*, 2016), such ecosystems are quickly vanishing from the Earth's surface (Silveira *et al.*, 2019; Pausas & Bond, 2020; Fernandes *et al.*, 2020). Thus, studies aiming to understand how herbivorous insects respond to human-induced disturbances are critical for conservation strategies of forest-grasslands mosaics and, consequently, a significant portion of the world's biodiversity.

Even minor impacts caused by anthropogenic disturbances in plant community structure, microclimatic conditions, and canopy cover should promote distinct influences on the stability of herbivorous insect communities (Wenninger & Inouye, 2008). This stability can be assessed by differences in herbivorous insect diversity patterns and composition across space and time. However, it is often much more complex to understand such influences when we consider communities interconnected by dispersal (i.e., metacommunities) as in forest-grassland mosaics (see da Silva *et al.*, 2019). In such systems, it is critical to understand the potential impacts of anthropogenic disturbances on both local and regional scales, which will determine the available pool of species to colonize the forest islands associated with the forest-grassland mosaics through spatial and temporal scales (Gilman *et al.*, 2010, Hellmann *et al.*, 2012). Additionally, assessing the influence of anthropic impacts on the internal structure of the forest islands, such as their canopy cover variation, is of great relevance, where a combination of historic and ecological processes may be acting together to dictate stability and diversity patterns of associated insect communities. In this context, it becomes imperative to evaluate how and why insect communities respond to the combination of cattle grazing and fire over time, which may help us understand the full effects of anthropogenic changes on our natural ecosystems (Oliveira *et al.*, 2014; Paolucci *et al.*, 2016), especially in the face of a hasty climate change scenario (Fonseca *et al.*, 2019).

Most disturbances with the potential to change biological patterns occur synergistically (Graham *et al.*, 2011). Despite this, some disturbances are more often studied as isolated events, such as cattle grazing (Yan *et al.*, 2015) and fires (Karavani *et al.*, 2018). The observed effects of cattle grazing on plant-herbivorous insect's network are mostly related to vegetation consumption, which leads to community compositional shifts, and, ultimately, changes in vegetation structure (Fleischner, 1994; Daskin *et al.*, 2016) that can last for many years (Daskin *et al.*, 2016). Despite the considerable knowledge on the effects of cattle grazing on the ground layer vegetation stratum (Balmer & Erhardt, 2000; Shapira *et al.*, 2020), it is still largely unknown its relation with other vegetation strata (but see Yan *et al.*, 2015). For instance, it is more likely that the understory's herbivorous insects will be more directly negatively affected by cattle grazing than the canopy ones. Additionally, we may need to consider the marked variations in microclimatic conditions among strata (Basset *et al.*, 2003). The adverse abiotic conditions found in the canopy throughout the year (e.g., high sun exposure and

wind speed) can act as strong filters for canopy-dwelling organisms, such as herbivorous insects (Shaw, 2004). Thus, any shift in such a drastic environment can lead to a complete extirpation of the canopy-associated insect fauna, implying that they are particularly vulnerable to disturbances by human activities (Stone *et al.*, 2018). Hence, spatial context is critical when evaluating the impact of anthropic disturbances, such as cattle grazing, on the functioning and dynamics of tropical ecosystems with forests with well-defined spatial structures (i.e., vertical stratification).

In forest ecosystems, fires are often considered a more acute and unpredictable disturbance than cattle grazing (chronic disturbances) (see Coelho *et al.*, 2018). Indeed, fire has been knowledge as a major agent of disturbance, acting across spatiotemporal scales and varying in frequency and magnitude, simplifying habitat structure through biomass removal (Bond & Keeley, 2005). Importantly, a fire in a forest can convert a closed habitat into a completely open one, disconnecting canopies and altering the microclimate conditions along the vertical strata (Abreu *et al.*, 2017; Andersen, 2019). Despite that, these shifts in habitat structure caused by the incidence of fire might be particularly strong for the herbivorous insect species living in forests understory, where changes in plant communities structure can be even more drastic (Vogel *et al.*, 2010). Climate change is predicted to alter the timing, severity, and frequency of fire events (Moritz *et al.*, 2012; Fonseca *et al.*, 2019). Therefore, understand how herbivorous insect communities respond to burning, and in which their stability can be altered in space and time is primordial for better account conservation needs in much greater detail for complex and key environments.

Understory and canopy insect species composition varies across light gradients associated with canopy-opening disturbances (Leach & Givnish, 1999), where open-habitat specialists may dominate recently disturbed habitats (Swengel, 2001). Therefore, canopy openness can be a strong indicator of the environmental conditions faced by the insect fauna. In ecosystems with a closed canopy, cattle can modify canopy traits by posing profound impacts on net primary production and its allocation between vertical strata (Altesor *et al.*, 2005). Similarly, severe fires can lead to a reduction of the tree canopy cover of fragments, resulting in dramatic and rapid understory plant community shifts (Miller & Safford, 2020; Stevens *et al.*, 2015). In this context, assessing spatiotemporal changes in herbivorous insect species composition can clarify both spatial and temporal scales of their stability (Anderson *et al.*, 2011; Baselga, 2010; Basset *et al.*,

2015; Neves *et al.*, 2021). This approach has considerable potential for addressing the influence of both cattle grazing and fire incidence but also canopy cover variation impacts on herbivorous insect communities across the forest's vertical strata. Ecological stability, the inverse of variation over time, is a fundamental ecosystem property that offers insights into biodiversity and ecosystem processes (Doak *et al.*, 1998; Tonkin *et al.*, 2017; Joseph *et al.*, 2019). Critically, temporal β -diversity can estimate colonizations (species gains) and extirpations (species losses) processes within a community over time (Tatsumi *et al.*, 2020, 2021), which provides complementary insights into community ecological stability and is essential to guide practical management decisions (Socolar *et al.*, 2016).

In this study, we asked whether the community stability of herbivorous insects, including their spatial distribution (vertical stratification), is influenced by canopy cover variation and/or anthropic disturbances (i.e., fire and cattle) over time in natural altimontane forest islands. We expect the stability of the herbivorous insect community (variation of species richness, abundance, and composition) to (i) be greater in the understory than in the canopy and (ii) decrease with greater variation in canopy cover, incidence of fire, and presence of cattle in the forest islands. We also expect that (iii) species gains would prevail over species losses through time in the understory while species losses would prevail over species gains in the canopy. Then, we evaluated the effect of canopy cover and anthropic disturbances in both species gains and losses, hypothesizing that (iv) greater variation in canopy cover as well as the incidence of fire and the presence of cattle in the forest islands would cause higher losses of species over time.

Materials and methods

Study area

This study was carried out in forest islands from a naturally formed montane forest archipelago immersed in an open matrix, situated in Serra do Cipó, a mountain complex within the southern portion of the Espinhaço Range Biosphere Reserve, Brazil (19°14'19"S, 43°31'35"W; Fig. 1). The Espinhaço is the most ancient and extensive mountain range at the South American eastern (Silveira *et al.*, 2016), with extreme relevance in terms of biodiversity and water resources in Brazil (Fernandes *et al.*, 2020).

It extends over 1200 km from southern Minas Gerais to the center of Bahia States, and it is amidst three great Brazilian biomes, the Caatinga (semi-arid) to its north, the Cerrado (Brazilian savanna) to its west, and the Atlantic Forest to its east; these last two are considered hotspots of biodiversity conservation (Myers *et al.*, 2000). Associated with these mountaintops and above 900 m a.s.l. we can find the *campo rupestre*, an ancient, climatically buffered, and diverse ecosystem that is considered the hottest Brazilian biodiversity hotspot and hosts various endangered and endemic species (Fernandes *et al.*, 2020; Hopper *et al.*, 2021). This ecosystem has a high edaphic and vegetational heterogeneity (Le Stradic *et al.*, 2015; Ferrari *et al.*, 2016) and enables the establishment of relictual forest islands, mainly at 1200 m a.s.l., that are associated with specific climate and soil parameters (Coelho *et al.*, 2018). These forest islands have a floristic composition similar to the seasonal semi-deciduous forests of the Atlantic Forest domain (Coelho *et al.*, 2018) with Myrtaceae, Lauraceae, Melastomataceae, and Fabaceae as the most common plant families. The regional climate is Cwb (dry-winter subtropical highland climate) according to Köppen's classification (Alvares *et al.*, 2013), with dry winters and rainy summers, a mean annual rainfall of 1500 mm and average annual temperature ranging from 17.4 to 19.8°C (data collected from a weather station installed at 1300 m a.s.l., near our study site: Onset HOBO® U30 data logger; Long-Term Ecological Research Program Project – PELD Campos Rupestres da Serra do Cipó; see Silveira *et al.*, 2019).

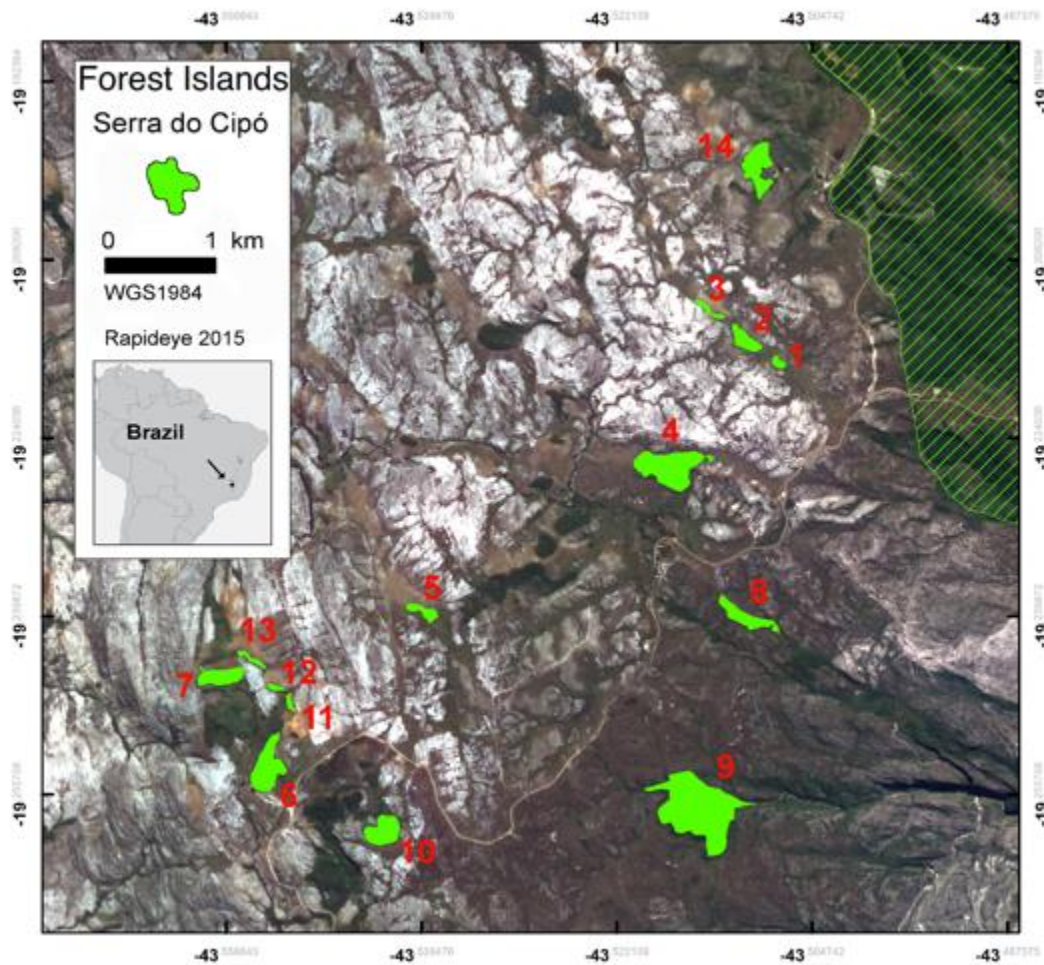


Figure 1. Map showing the 14 naturally-fragmented forest islands (green shapes) where we sampled herbivorous insects in a campo rupestre matrix of the Serra do Cipó, southern portion of the Espinhaço Range Biosphere Reserve, Minas Gerais, Brazil.

Sampling design

We selected 14 forest islands that belong to the permanent plots of the Long-Term Ecological Research Project *Campos Rupestres*. The chosen forest islands vary in size (1.21–39.89 ha, mean = 8.21 ha, SD = 10.24 ha) and shape (from circular to elongated limits), and are spaced at variable distances (0.1–1.5 km) from each other (Fig. 1). A 20 × 50 m plot was established in the center of each forest patch, where was performed a four-year sampling in the rainy season of 2014, 2015, 2018, and 2020. In each sampling period, we collected herbivorous insects using two Malaise traps (one soil Malaise trap and one canopy Malaise Window trap) located in the center of each plot, which remained in the field for seven days (9408 trap-hours for each type) (see Perillo *et al.*, 2020 for details). These trap models have different sampling efficiency, disfavoring comparison

of insect diversity between strata. However, it allows us to effectively compare the temporal changes in insect diversity and composition in vertical dimensions. We considered as herbivorous insects every insect belonging to families that directly or indirectly depend on plant resources for survival (Moran & Southwood, 1982; Kuchenbecker *et al.*, 2021). The insects were identified using taxonomic keys and separated into morphospecies based on external morphological features. All collected insects were stored in the entomological collection of the Laboratory of Insect Ecology at the Federal University of Minas Gerais (Universidade Federal de Minas Gerais - UFMG). In each field campaign, we also took five 1.5 m height hemispherical photos with a fish-eye lens attached to a digital camera (Canon EOS Rebel T5i), one at each of the four plot vertices and one at the center of the plot to estimate canopy cover (see Nassar *et al.*, 2008). Finally, we estimated the incidence of fire and the presence of cattle in each plot at the end of the dry season of each year, carrying detailed observations based on the presence/absence of remains of recently burned vegetation and the presence of cattle feces.

Canopy variation

To evaluate the temporal variation of the canopy cover, the hemispherical photos taken were processed for the proportion between white and black pixels. Average values from the five photos (taken from the five points of each plot) were used to obtain a single canopy cover value for each forest island. The “ReadImages” (Oles *et al.*, 2015) and “RT4Bio” (Reis Jr *et al.*, 2015) packages were used to separate the white and black points of each photo and define the variation of the canopy coverage within the *Capões de Mata*. All photos were processed using R software v.4.0. (R Core Team, 2022).

Data analysis

In order to show extrapolated values of species richness to a similar number of individuals we constructed rarefaction curves using the R package ‘iNEXT’ (Chao *et al.*, 2014; Hsieh *et al.*, 2016), available at <https://chao.shinyapps.io/iNEXTOnline/>. We accounted for every individual collected in the two Malaise traps. Thus, we estimated the sample completeness about each individual sampled. For extrapolation curves, the number of individuals was up to twice the actual reference size (Chao *et al.*, 2013).

We performed separate analyses for the understory and canopy species along four sampling dates over seven years. To measure the stability of the herbivorous insect community, we calculated the variation in richness and abundance of herbivorous insect species in each stratum for each forest island between Time 1 and Time 2 according to the sequence of samplings (2014–2015, 2015–2018, 2018–2020). Also, the dissimilarity (i.e., β -diversity) in the composition of herbivorous insects in each stratum was measured for each forest island between Time 1 and Time 2 (2014–2015, 2015–2018, 2018–2020) using the Temporal Beta-diversity Index (TBI) approach (see Legendre, 2019). This approach allows to calculate species loss and gain components of the dissimilarity. The TBI value can be decomposed into two components: B = species losses and C = species gains (Legendre & Condit, 2019). Then, B and C statistics are used to produce B - C plots, with B (losses per forest island) in the abscissa and C (gains per forest island) in the ordinate (Legendre, 2019). B - C plots display visually the relative importance of the key processes of insect losses and gains across the forest archipelago, through time, in space-time surveys (Legendre & Condit, 2019). We used the Sorensen dissimilarity for incidence data to calculate the pairwise dissimilarities. The mean of the differences between the B and C statistics is also computed across all forest islands to herbivorous insects in each stratum (i.e., canopy and understory). A positive value of $[C - B]$ indicates that the forest archipelago stratum was dominated by gains, whereas a negative value indicates overall losses of species (Legendre, 2019). The $[C - B]$ difference across all forest sites strata was tested for statistical differences using a paired t -test computed for the C and B statistics from all forest islands. The calculations were carried out using the “TBI” and “plot.TBI” functions of the R package “adespatial” (Dray *et al.*, 2020).

We used separate Generalized Linear Mixed-effect Models (GLMMs) to test for effects on the variation of species richness, abundance, temporal beta diversity index, species gains and species losses among years of sampling, and related to canopy cover variation and disturbances variables (total canopy variation coefficient over the four samplings, vertical strata, fire incidence, and cattle presence). The identity of forest islands (14 in total) was used as random factor to account for temporal pseudoreplication (Bolker *et al.*, 2009). We used the Gaussian distribution for the components of gains and losses, using the functions “lmer” of the R package “lme4” (Bates *et al.*, 2015) for these models. The function “Anova” of package “car”, which allows ANOVA in mixed models, was used to deem variables significant or not. All models were subjected to residual

analyses to check for model fit and error structure suitability (Crawley, 2013). All statistical analyses were performed using R software v.4.0. (R Core Team, 2022).

Results

General patterns

Between 2014 and 2020, we sampled a total of 5567 herbivorous insects belonging to 50 families and 655 morphospecies (Table 1). Among the sampled families, Cicadellidae, Chrysomelidae and Curculionidae were the richest in species (114, 90, and 75 respectively) and most abundant (3197, 767, and 290 respectively), with the Cicadellidae family alone representing 17.4% and 57.4% of the total richness and abundance, respectively. There was also a high number of rarely sampled species, comprising 303 singletons (46.3% of the total) and 108 doubletons (16.5% of the total). In addition, we had a greater number of unique morphospecies collected in the understory. A total of 449 (68.5%) morphospecies were collected exclusively in the understory, while 88 (13.4%) were collected exclusively in the canopy and 118 (18.1%) in both strata.

Table 1. Herbivorous insects morphospecies richness (rich) and abundance (abund) sampled in the understory (und) and canopy (can) strata in Serra do Cipó, Minas Gerais, Brazil.

Taxa	Family	Stratum rich		Stratum abund		Total diversity	
		Und	Can	Und	Can	Abund	Rich
Auchenorrhyncha	Achilidae	25	4	134	11	145	25
	Aetalionidae	1	NA	1	NA	1	1
	Aphrophoridae	1	NA	1	NA	1	1
	Cercopidae	5	1	5	1	6	6
	Cicadellidae	108	33	3021	176	3197	114
	Cicadidae	1	2	1	3	4	3
	Cixiidae	16	4	29	4	33	17
	Cydnidae	1	NA	7	NA	7	1
	Delphacidae	6	1	17	6	23	7
	Derbidae	4	3	96	3	99	4
	Fulgoridae	1	NA	9	NA	9	1
	Issidae	2	NA	5	NA	5	2
	Membracidae	17	4	45	4	49	19
	Anobiidae	12	10	25	25	50	19
Coleoptera	Anthribidae	22	6	34	10	44	25
	Attelabidae	1	NA	1	NA	1	1

Heteroptera	Bostrichidae	5	8	10	14	24	11
	Brentidae	6	1	7	2	9	7
	Buprestidae	10	2	42	2	44	11
	Cerambycidae	37	17	86	46	132	47
	Cerophytidae	1	NA	1	NA	1	1
	Chrysomelidae	85	23	660	107	767	90
	Cupedidae	1	4	1	5	6	5
	Curculionidae	68	21	258	32	290	75
	Elateridae	26	23	161	60	221	35
	Erotylidae	4	NA	5	NA	5	4
	Hydraenidae	1	NA	1	NA	1	1
	Megalopodidae	1	NA	1	NA	1	1
	Mordelidae	12	3	49	3	52	13
	Berytidae	1	NA	4	NA	4	1
	Largidae	1	NA	1	NA	1	1
	Lygaeidae	7	1	23	1	24	7
	Miridae	20	10	32	10	42	26
	Pentatomidae	5	NA	5	NA	5	5
	Pyrrhocoridae	1	NA	1	NA	1	1
	Rhopalidae	1	1	1	1	2	2
	Scutelleridae	NA	1	NA	1	1	1
	Thyreocoridae	1	NA	1	NA	1	1
	Tingidae	8	NA	18	NA	18	8
	Acrididae	3	NA	15	NA	15	3
Orthoptera	Anostomatidae	1	NA	1	NA	1	1
	Eumastacidae	2	2	2	2	4	4
	Gryllidae	1	NA	1	NA	1	1
	Oecanthidae	NA	1	NA	1	1	1
	Ommexechidae	1	NA	1	NA	1	1
	Romaelidae	4	NA	4	NA	4	4
	Tettigoniidae	2	1	7	1	8	3
	Trigonidiidae	2	1	4	1	5	2
Sternorrhyncha	Aphididae	2	1	2	1	3	2
	Psyllidae	24	17	164	34	198	33

The sampling effort was sufficient to characterize the insect community sampled, with the rarefaction-extrapolation accumulation curves presenting a greater sampling coverage for those carried out in the understory (Supplementary Figure 1), where the observed and extrapolated insect richness and abundance was higher than in the canopy. Species richness ranged between 206 and 567 species and its total abundance ranged between 567 and 5000 specimens, which corresponds to 78% and 95% of the sampling coverage values along the canopy and the understory respectively (extrapolated sample coverage richness = 304 and 755 along the canopy and the understory, respectively).

Herbivorous insects' community stability

The herbivorous insect community was more temporally stable in the understory than in the canopy, showing an evident stratification according to data on the variation of species richness, abundance, and composition (TBI) (Table 2). In this regard, the canopy presented higher values for temporal diversity variation of herbivorous insects and lower values for the variation of species richness and abundance than the understory (Fig. 2).

Table 2. Generalized Linear Mixed Models showing the effects of the independent variables (fire, presence of cattle, strata, and canopy cover variation) on the variation of herbivorous insect species richness, abundance and temporal beta diversity index. Pr(>F) values at or below 0.05 are deemed significant and are indicated in bold face.

Dependent variables	Independent variables	Df	F-value	Pr(>F)
Δ Richness	Incidence of fire	1	1.8765	0.1754
	Presence of Cattle	1	0.7369	0.4088
	Vertical strata	1	9.2399	0.0036
	Canopy cover variation	1	0.5787	0.4496
Δ Abundance	Incidence of fire	1	2.7680	0.1009
	Presence of Cattle	1	0.0834	0.7781
	Vertical strata	1	9.2399	0.0036
	Canopy cover variation	1	0.2871	0.5940
TBI	Incidence of fire	1	44825	0.0383
	Presence of Cattle	1	49608	0.0508
	Vertical strata	1	608145	<0.0001
	Canopy cover variation	1	1.0566	0.3087

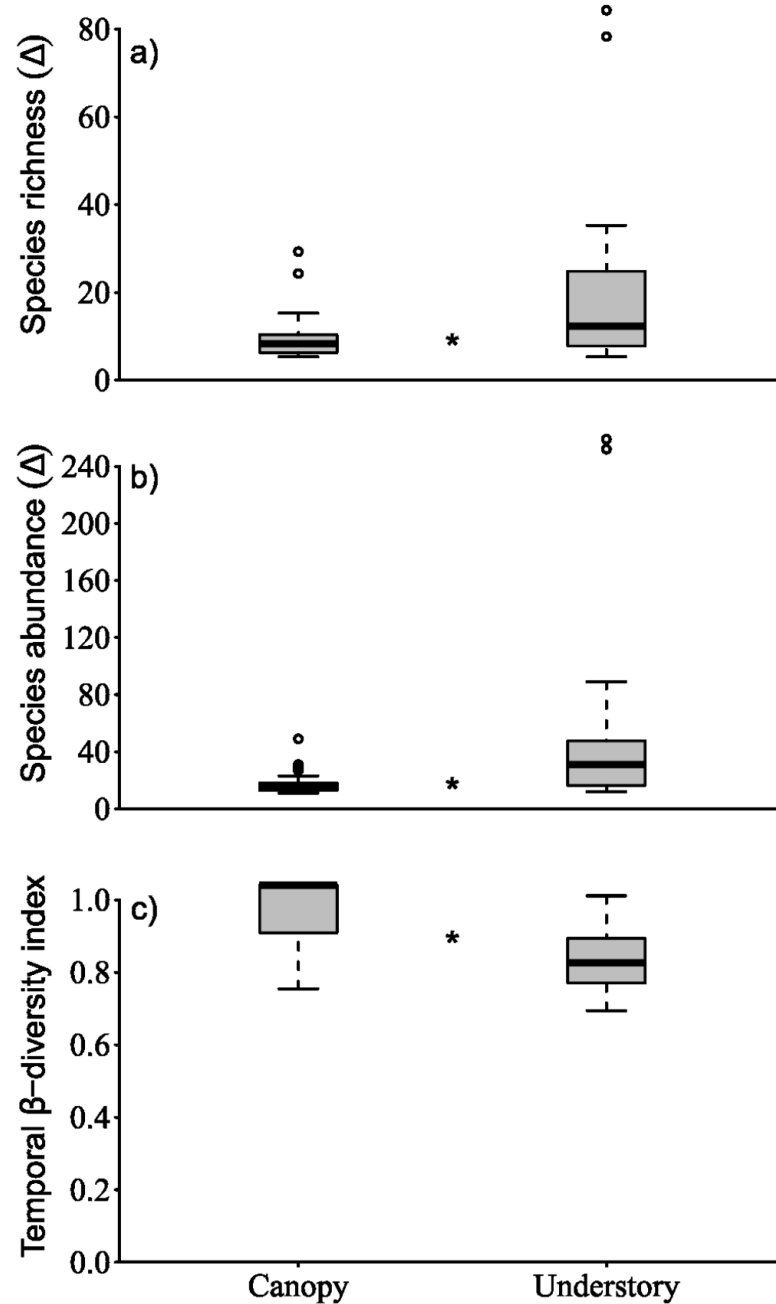


Figure 2. Boxplots of variation of herbivorous insect species a) richness, b) abundance and c) temporal diversity variation in the canopy and understory strata of forest islands at the Espinhaço Range, southeastern Brazil. Stars reflect significant differences ($p < 0.05$) between strata.

Neither canopy cover variation (Supplementary Figure 2) nor anthropic disturbances (Fig. 3 for fire incidence and Supplementary Figure 3 for cattle presence) influenced the variation of species richness and abundance (Table 2). Similarly, canopy cover variation

(Supplementary Figure 2) and the presence of cattle (Supplementary Figure 3) did not influence the temporal beta diversity of herbivorous insects either (Table 2). Only the incidence of fire had an effect on insect temporal composition variation, with forest islands with no fire showing higher values of temporal beta diversity of herbivorous insects (Table 2, Fig 3).

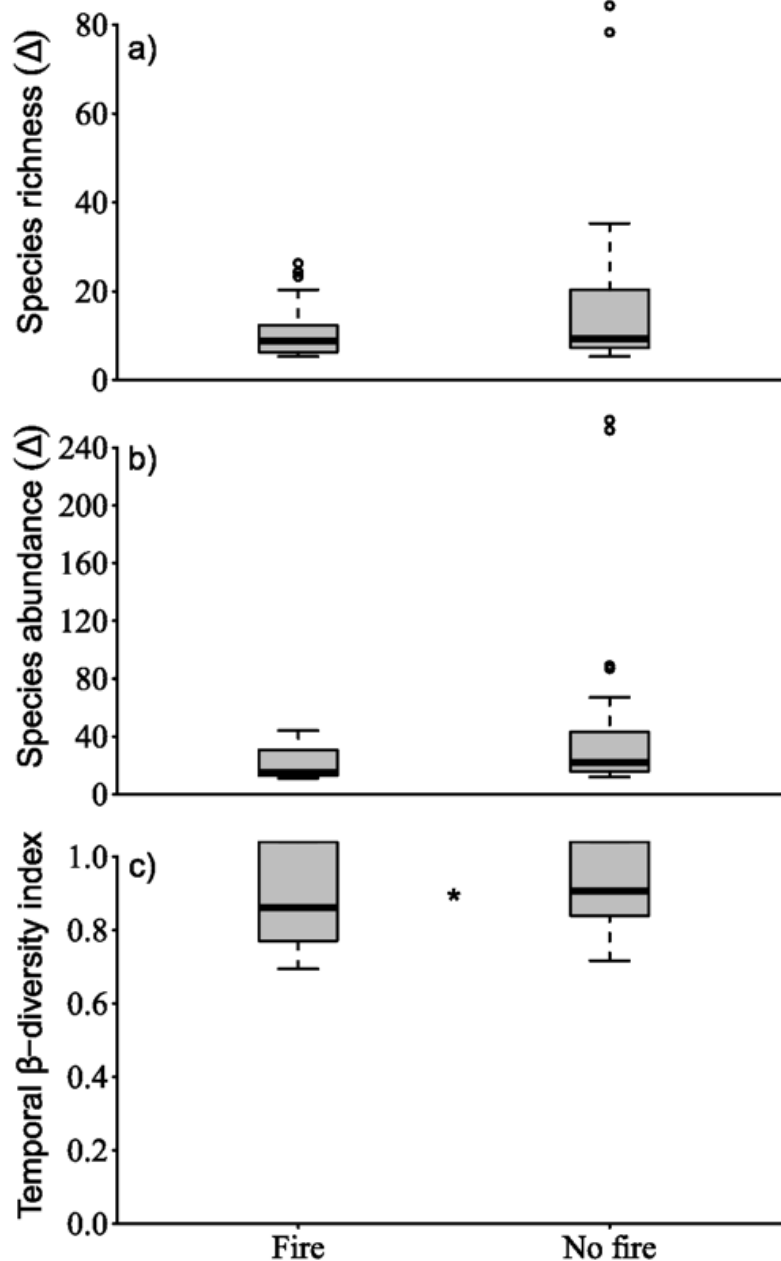


Figure 3. Boxplots of variation of herbivorous insect species a) richness, b) abundance and c) temporal diversity variation in forest islands at the Espinhaço Range, southeastern Brazil, with and without fire incidence. Stars reflect significant differences ($p < 0.05$) between forest islands with and without fire incidence.

Species gains and losses

According to TBI analysis, we found species compositional changes between understory and canopy among all pairwise combinations of consecutive sampling years (i.e., 2014–2015, 2015–2018, and 2018–2020). Initially, we had more species losses than gains (2014-2015), followed by a dominance of species gains (2015-2018), and, finally, followed by more species losses than gains (2018-2020) (Supplementary Figure 4). Both strata showed a similar general pattern of species compositional changes. However, the species gains were more pronounced in the canopy (Fig. 4, Table 3).

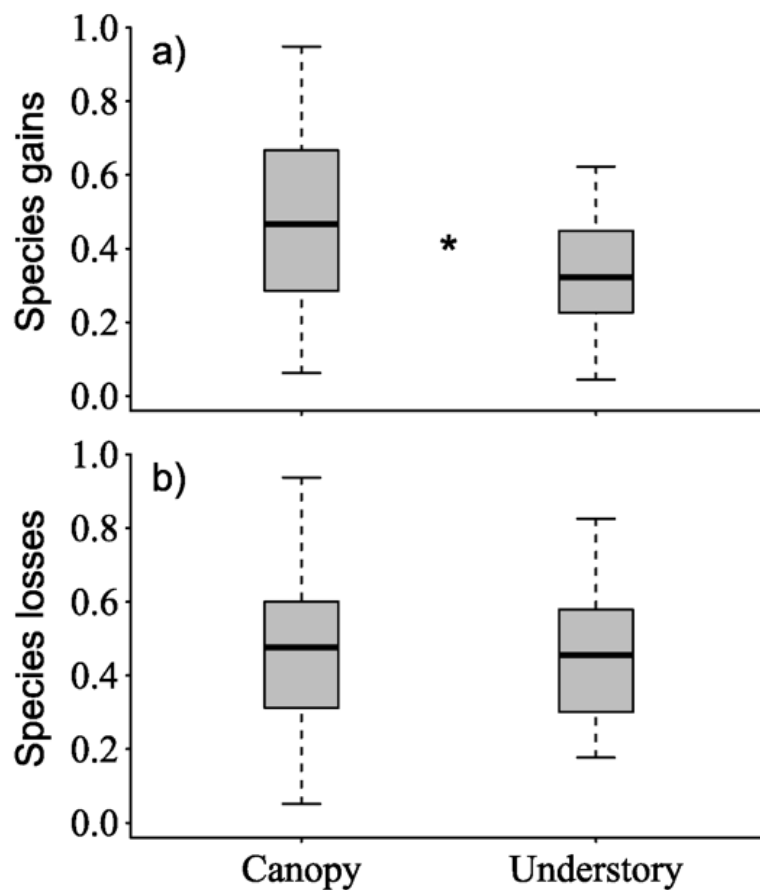


Figure 4. Boxplots of herbivorous insect species a) gains and b) losses in the canopy and understory strata of forest islands at the Espinhaço Range, southeastern Brazil. Stars reflect significant differences ($p < 0.05$) between strata.

Table 3 | Generalized Linear Mixed Models showing the effects of the independent variables (fire, presence of cattle, strata, and canopy cover variation) on the herbivorous insect species gains and losses. $\text{Pr}(> F)$ values at or below 0.05 are deemed significant and are indicated in bold face.

Dependent variables	Independent variables	Df	F value	$\text{Pr}(> F)$
Species gains	Incidence of fire	1	0.6539	0.4219
	Presence of Cattle	1	0.1328	0.7222
	Vertical strata	1	7.9860	0.0064
	Canopy cover variation	1	8.1192	0.0069
Species losses	Incidence of fire	1	0.0436	0.8352
	Presence of Cattle	1	1.7495	0.2113
	Vertical strata	1	0.0913	0.7636
	Canopy cover variation	1	7.663	0.0085

The total canopy variation coefficient over a seven years interval (within four sampling periods) was important for explaining both species gains and losses (Table 3), where higher numbers of species gains were associated with higher canopy cover variation, and higher numbers of species losses were associated with lower canopy cover variation (Fig. 5).

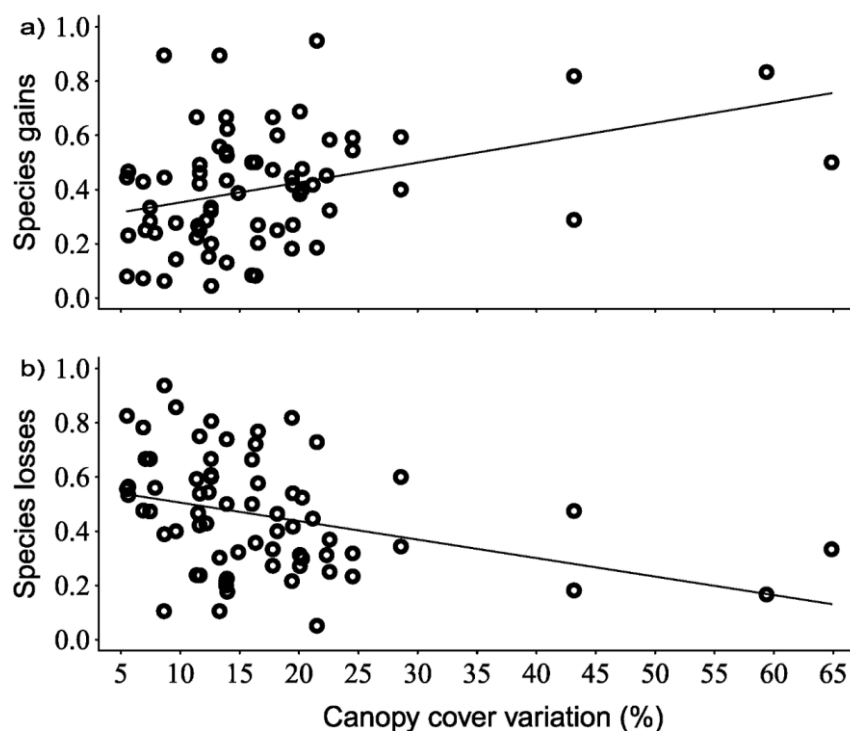


Figure 5. Effect of canopy cover variation on the herbivorous insect species a) gains and e) losses of forest islands at the Espinhaço Range, southeastern Brazil.

We found no effect of anthropic disturbances (i.e., incidence of fire and presence of cattle) in herbivorous insect species gains and losses on forest islands (Table 3; Supplementary Figures 5 and 6).

Discussion

Although a vast body of literature has focused on the effects of anthropic disturbances, such as cattle grazing and human-induced fires, on plant communities and population dynamics (Pilon *et al.*, 2018; Bonilla-Valencia *et al.*, 2020; Malanson *et al.*, 2021), much less attention has been given to how such disturbances influence not only species at higher trophic levels, like herbivorous insects, but also their distribution in different strata of vegetation. Here we evaluated the potential influence that both cattle presence and fire incidence, as well as canopy cover variation, have on the spatiotemporal distribution of herbivorous insect communities between different forest islands and within these islands, into the vertical strata. For this, we studied a critically endangered ecosystem comprised of mountainous tropical forest islands immersed in a grassland-dominated matrix. Fire was the only variable that influenced the stability of herbivorous insects, with forest islands with no fire showing a greater variation of insect communities over time. We also evaluated which factor contributed more to the species loss and gains, and found that it was mainly explained by canopy cover variation. Importantly, in the canopy the gains were higher than the losses during the seven years covered in our study. Besides, as expected, the understory was more temporally stable than the canopy, with a smaller variation of herbivorous insect communities over time. Overall, we argue that our study brings critical insights on the role of anthropic disturbances on the spatiotemporal dynamics of herbivorous insects, focusing on differences between different forest patches and vertical strata.

The observed higher species stability in the understory than in the canopy is concordant with a previous study in the same area, where the understory had more diverse and stable herbivorous insect communities between seasons (Kuchenbecker *et al.*, 2021). These findings – a consistently higher canopy beta diversity compared to the understory – suggest that these communities may operate at different scales. Indeed, the pronounced

vertical axis present in forest ecosystems creates gradients of several abiotic and biotic factors (Nakamura *et al.*, 2017), which probably influence the associated insect fauna communities (see da Silva *et al.*, 2019; Perillo *et al.*, 2020; Brant *et al.*, 2021). For example, the higher sun exposure and wind speed in the canopy generate greater abiotic stress in those environments (Parker, 1995; Shaw, 2004), making them more prone to more drastic shifts in microclimatic conditions and insect communities through time than the understory. These drastic shifts may also explain the smaller variation that we found in both herbivorous insect species richness and abundance associated with canopy environment over the seven years of sampling. As it faces extreme abiotic conditions throughout the entire year, canopy has leaves and branches that are physiologically and structurally adapted, differing from those in lower strata (Ulyshen, 2011). Thus, it is reasonable to expect that the canopy in these montane forest islands has a specific range of associated herbivorous insects that are more adapted to such more adverse conditions, consequently having its diversity less variable when compared to the understory.

Ecological processes, such as environmental filtering, are able to change the spatial variation in species compositions through time (Chase, 2003; Mouquet & Loreau, 2003; Fukami, 2015) and can also be related to the increase or decrease in response to both species' gains or losses (Olden *et al.*, 2004; Olden & Rooney, 2006; Socolar *et al.*, 2016). In particular, variation in herbivorous insect communities across forest strata has been associated with temporal changes in forest heterogeneity of micro-environmental conditions (Murakami *et al.*, 2005). For example, the canopy cover variation in the forests islands over time can provide a temporally more heterogeneous micro-environment for the herbivorous insects. Because this stratum constantly offers more new leaves, flowers, fruits and, consequently, more resources (Basset *et al.*, 2003), a variation on resource offer can result in a pattern of more generalist species gains in the canopy. This may be directly related to our findings of higher species gain values for the canopy associated with greater variation in canopy cover over the years. It is worth mentioning that despite the canopy gaining more species, it probably loses species in the same proportion due to the adverse conditions' characteristic of this vegetation stratum that limits the number of insects adapted to this environmental filter. However, an important and core issue is to understand from where these species that are arriving are coming from. These patterns that we found of both species' diversity as well as colonization and extirpation processes can be reflecting locally (i.e., forest strata) and regionally (i.e., adjacent forest islands)

organized networks linked by dispersal (i.e., metacommunities) (see Mouquet & Loreau, 2003; Neves *et al.*, 2021). A recent study carried out with groups of birds in forest patches reinforces this possibility, where bird–plant interactions involving birds feeding on and under-the-tree had a major contribution to metanetwork organization (Li *et al.*, 2020). In this way, the local immigration of herbivorous insects experienced by the canopy may be mostly composed by generalist species coming from the lower stratum or even from the nearest forest islands that are constantly connected by dispersal events.

Microclimatic conditions and distribution of potential resources that affect herbivorous insect community organization and diversity may also be altered by anthropogenic activities (Fibich *et al.*, 2016), which are able to provoke marked differences in sunlight radiation and resource availability. Here we found that herbivorous insect communities varied less over time on forest islands with fire records, which can lead to negative effects on ecosystem functioning and stability (Cardinale *et al.*, 2012) mostly due to altered feedback dynamics between plants and their consumers (Kim & Holt, 2012). For example, fire can directly impact consumer communities through both herbivorous insect mortality and their movement out of the habitat (Swengel, 2001). Additionally, fire effects on herbivorous insects can also be indirect, affecting the short- and long-term temporal availability of resources post-fire (Swengel, 2001). However, it is worth mentioning that understory density usually increases after fire events, supplying previously impaired resource availability which ends up favoring more generalist species (Devine *et al.*, 2015). This is probably the reason why we did not find an effect of fire on herbivorous insect diversity variation over the years nor on the colonization and extirpation processes. In fact, some studies on fire-sustained systems have been demonstrating the regulation of herbivorous insect species by bottom-up forces (Marques *et al.*, 2000; Wenninger & Inouye, 2008). Although studies examining fire effects on herbivorous insects are still relatively scarce (but see Vieira *et al.*, 1996; Kerstyn & Stiling, 1999), some have shown that this disturbance has a considerable effect on herbivorous insect communities mainly through changes in habitat structure, including canopy openness (Kay *et al.*, 2007; Kim & Holt, 2012). Therefore, we can argue that fire act as an important anthropic environmental filter, shaping the structure of herbivorous insect communities associated with tropical montane forest islands.

Large herbivores are commonly related to plant density reduction through trampling and consumption, reducing resource availability for herbivorous insects and

generating smaller and more fragile plant-insect networks. Indeed, high cattle grazing intensity has a significant impact on decreasing plant species composition and abundance (Mtimbanjayo & Sangeda, 2018). However, under low intensity, cattle grazing may have positive effects on plant communities by elevating plant diversity (e.g., by suppressing dominant competitors) (Olf and Ritchie, 1998), and avoiding fire-mediated canopy openness (Kuchenbecker *et al.*, *in press*) or have no effect at all (Mtimbanjayo & Sangeda, 2018). Here we found no influence of cattle grazing on herbivorous insect species diversity or composition, corroborating some other studies that demonstrate that moderate grazing pressure can even be used to restore or maintain native plant communities and associated species (see Zakkak *et al.*, 2014), which might foster larger and more stable plant-insect networks.

Considering the major pressure of climate change on tropical altimontane forest systems (Nunes *et al.*, 2020), it becomes a priority that we understand the response of a given consumer species assemblage to anthropic disturbances and local-scale changes mediated by them. It gives us an interplay of multiple processes that directly and indirectly affect in situ survival, recolonization, within-patch community dynamics, and consequently, conservation planning. Complementarily, the comprehension of dynamics underlying the stability of communities provides a robust way to predict how the organization of biodiversity and ecosystem functionality will change in response to further environmental and climatic changes (Tatsumi *et al.*, 2020). Spatiotemporal dynamics of species composition variation are then useful for a better understanding of the spatial processes and patterns of metacommunities through time (Leibold & Chase, 2017).

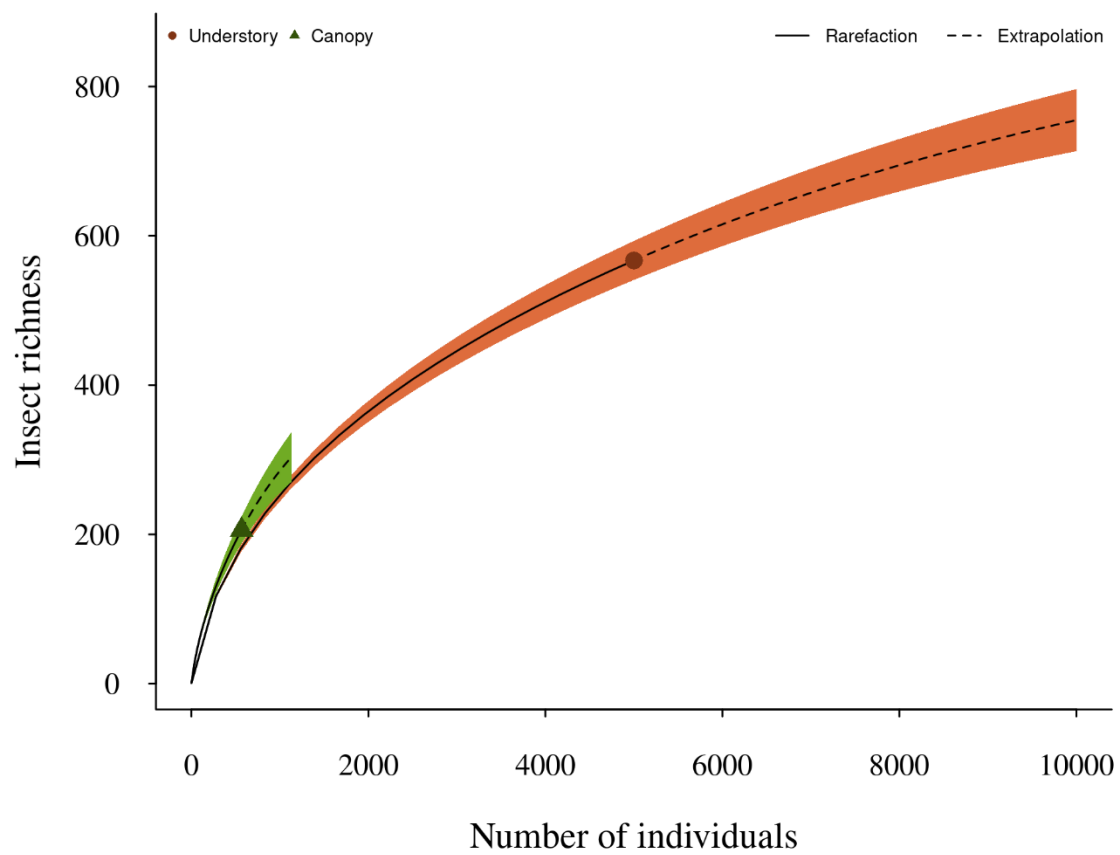
It is not trivial that ecological factors and intrinsic biological characteristics of herbivorous insects can influence their patterns of distribution and diversity, resulting in two distinct insect communities along vertical stratification. We draw attention to cattle grazing not being detrimental to the stability of herbivorous insect communities, reiterating previous findings of the effect of cattle on the presented forest islands (Kuchenbecker *et al.*, *in press*). However, careful studies should be performed to check the effects of cattle grazing on insect communities and whether this practice is indeed a biodiversity-friendly approach under low densities. Finally, we found different filters acting in different ways in herbivorous insect communities present in distinct strata. We provide new insights to help to understand metacommunity-scale species interactions,

which have considerable relevance to the conservation of ecosystem functioning in already naturally threatened systems. The success or failure of conservation actions in this forest-grassland mosaic largely depends on a better understanding of temporal variation and new insights into ecological community structure across space and time of the organisms that inhabit them. Concerted action must be made to protect these natural refugees against pervasive stressors.

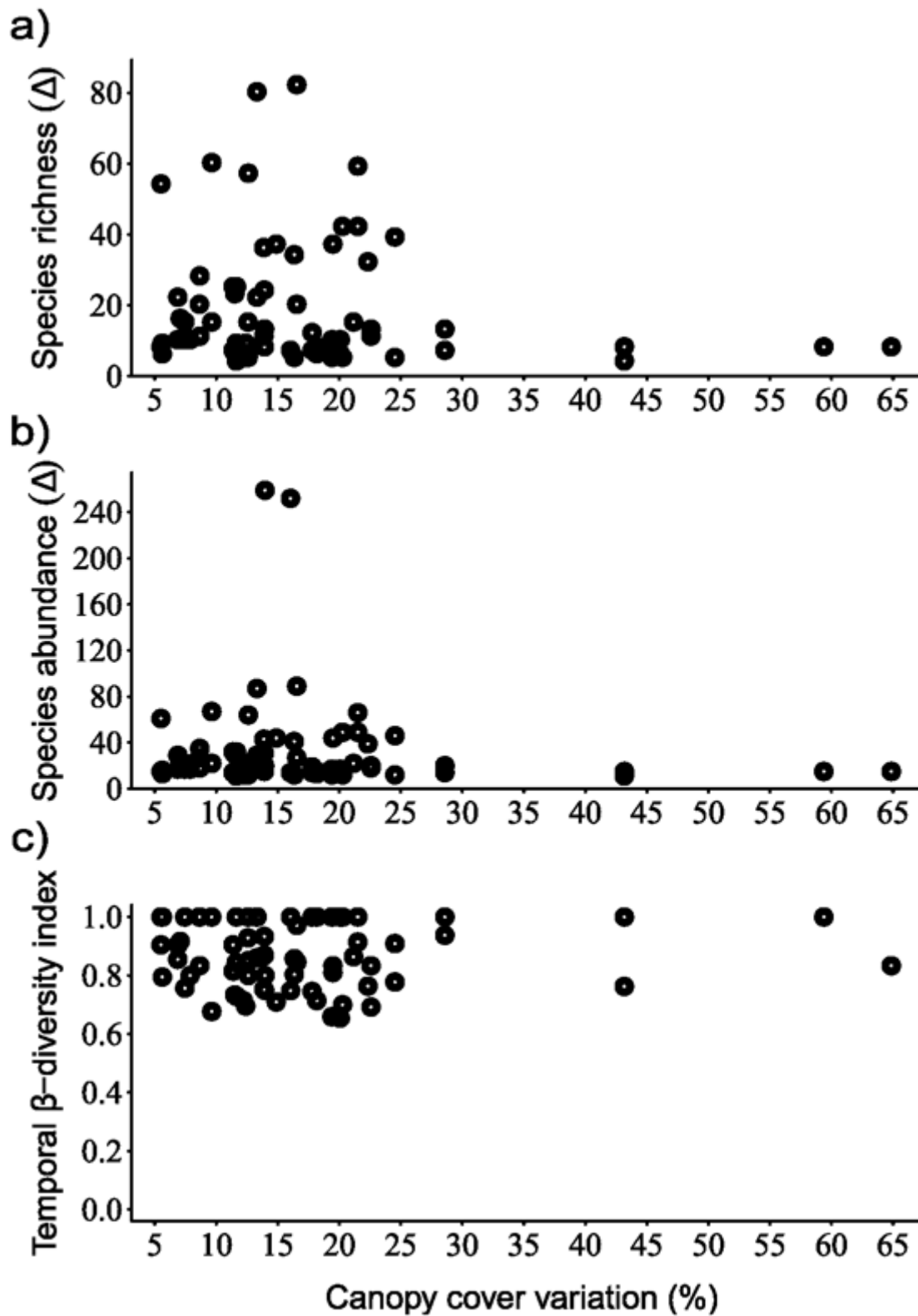
Acknowledgments

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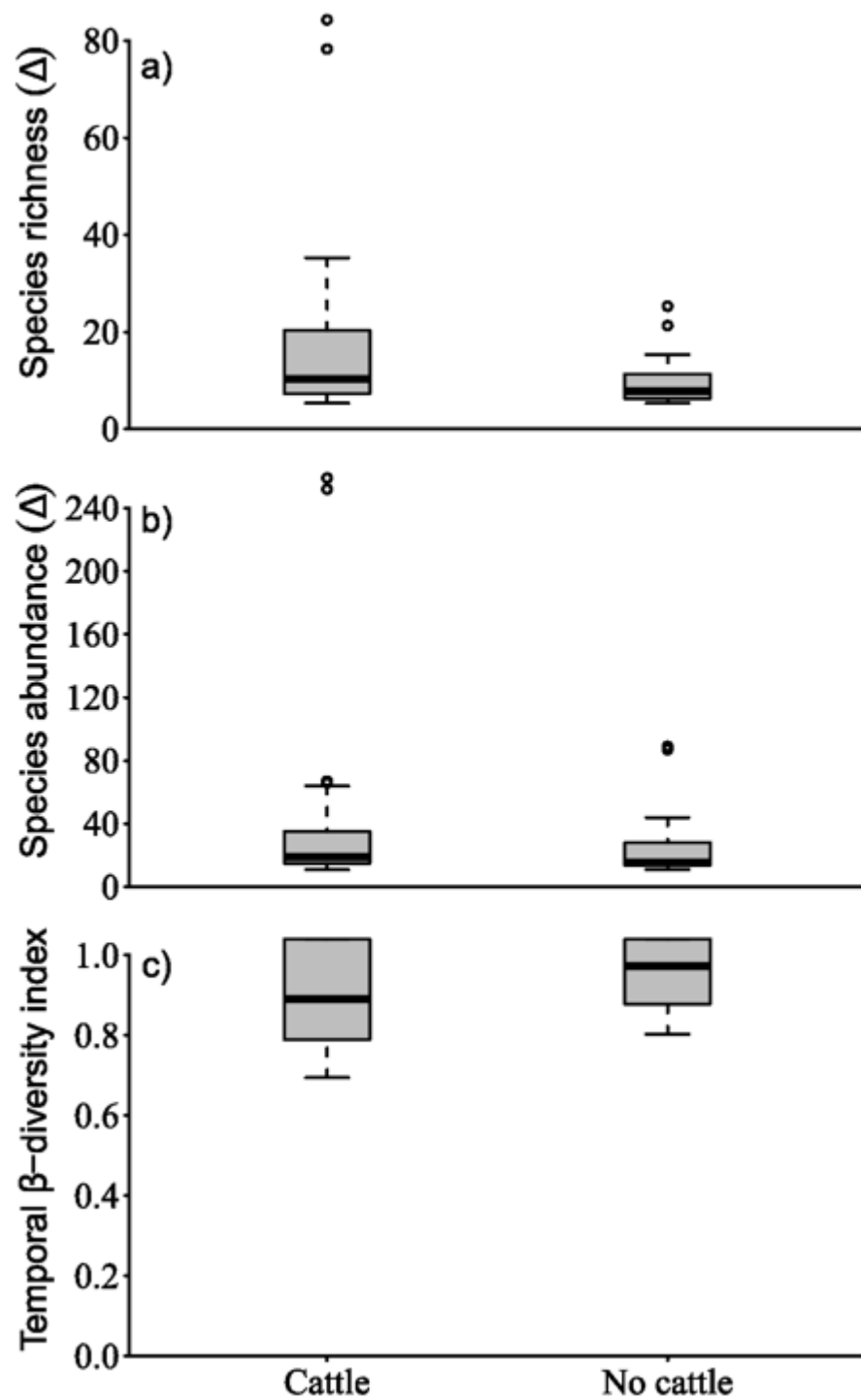
Supplementary material



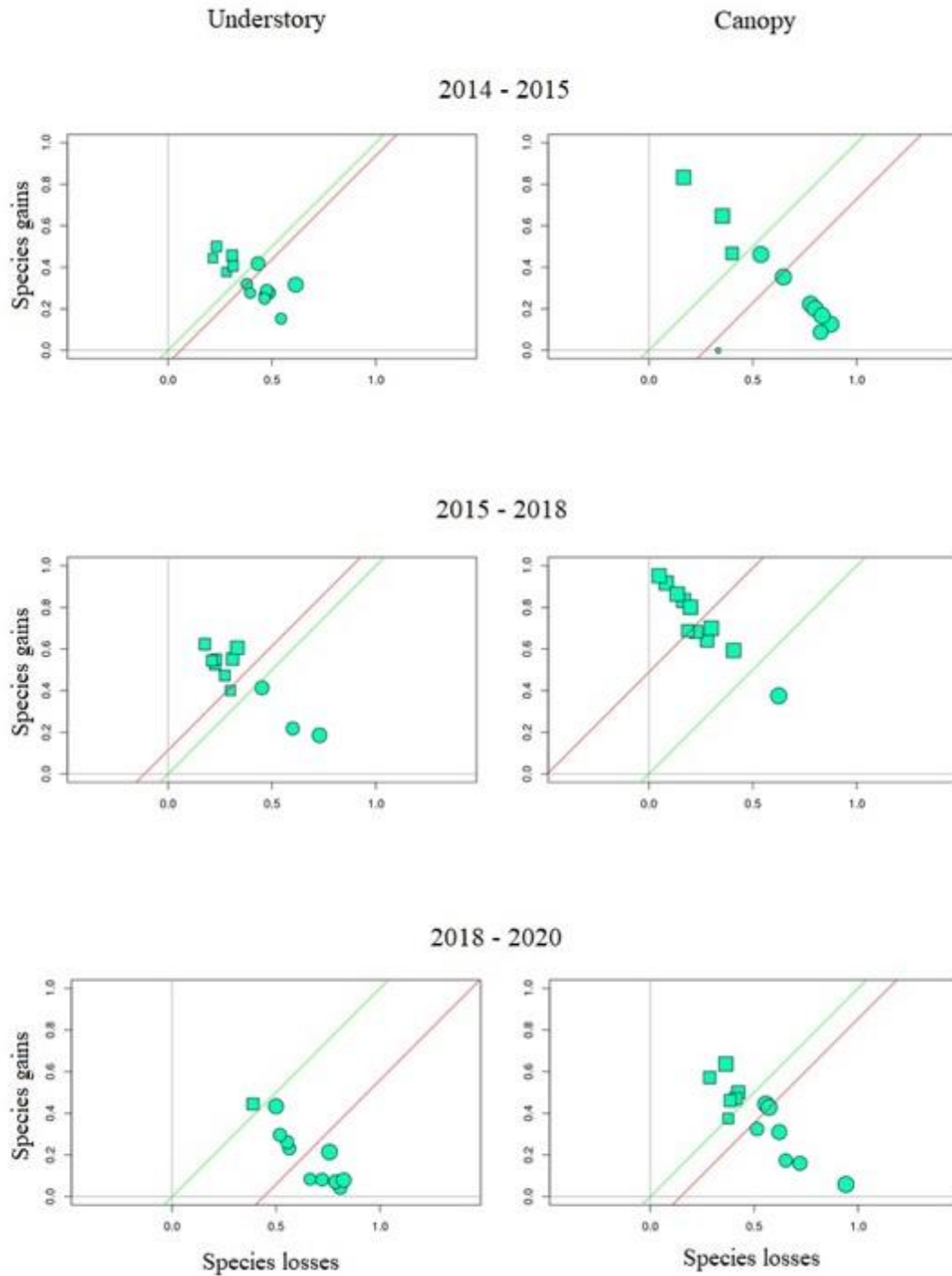
Supplementary figure 1. Species diversity curves (0D) for samples (solid lines) and extrapolated samples (dashed lines) as a function of sample size according to the count of incidences of herbivorous insects in each stratum (i.e., understory and canopy) of forest islands at the Espinhaço Range, southeastern Brazil. The red circle in the red line represents the observed samples for understory and the green triangle for the canopy, obtained by a bootstrap method based on 1000 interactions.



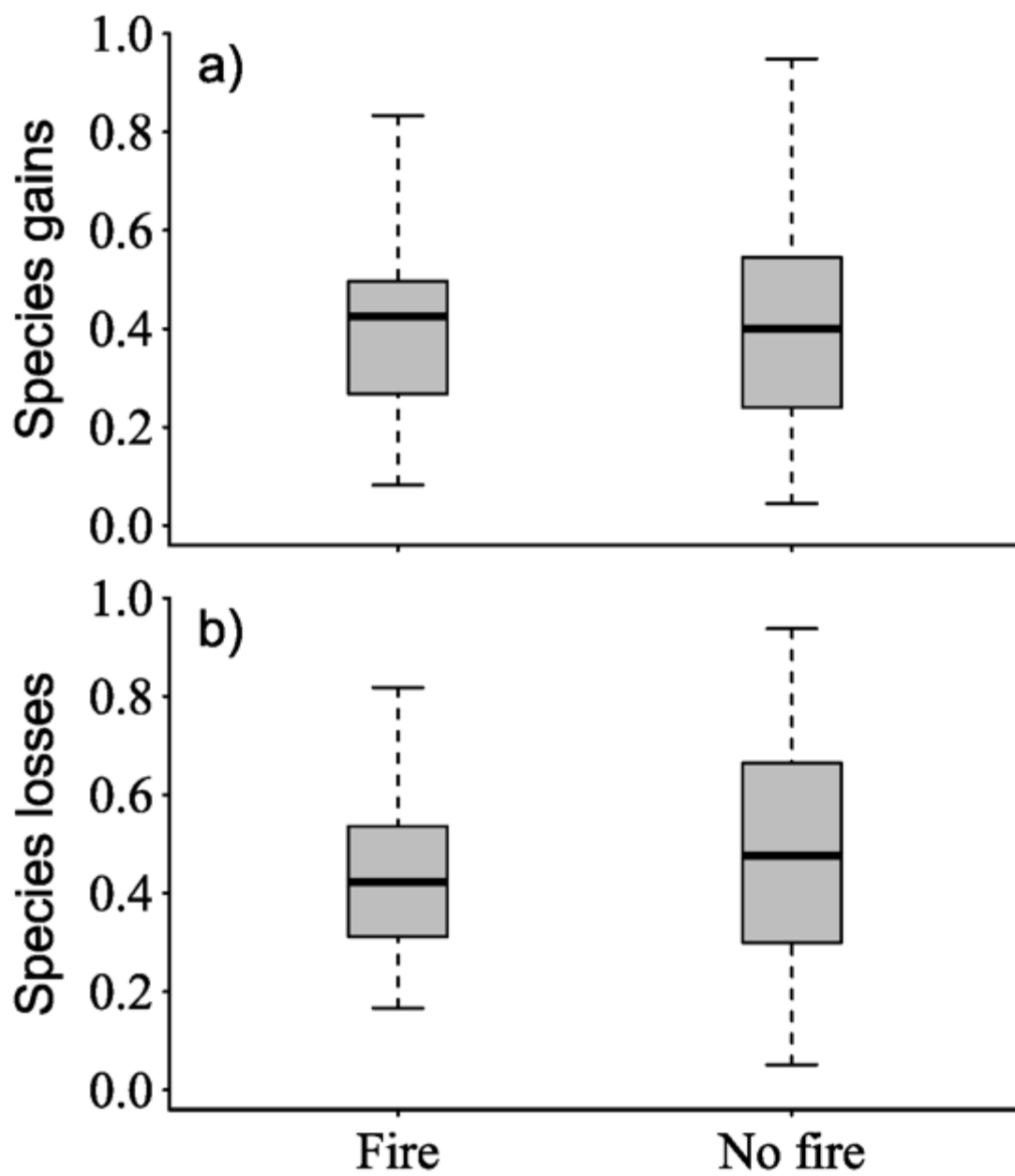
Supplementary figure 2. Effect of canopy cover variation on the variation of herbivorous insect species a) richness, b) abundance and c) temporal diversity variation of forest islands at the Espinhaço Range, southeastern Brazil.



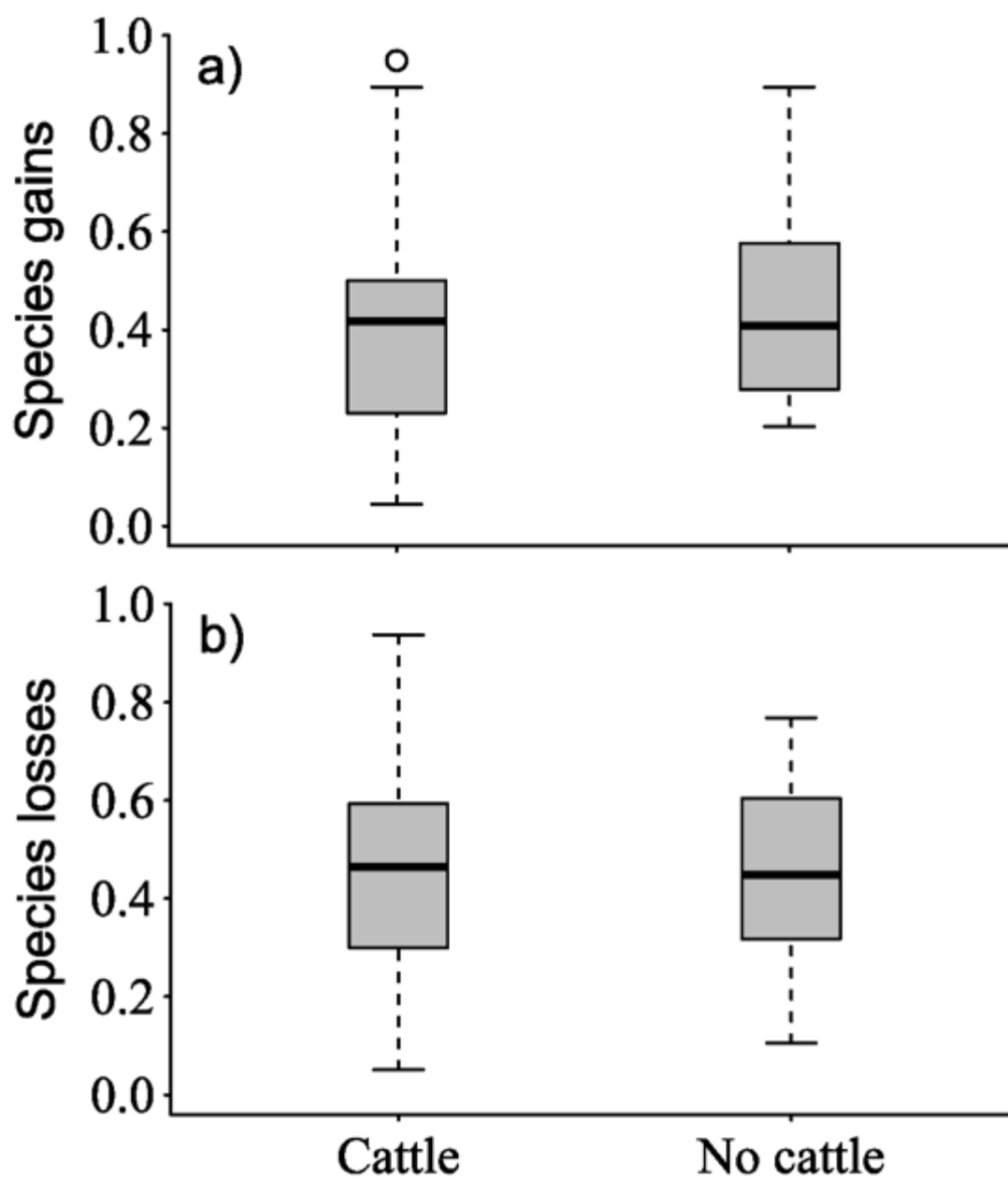
Supplementary figure 3. Boxplots of variation of herbivorous insect species a) richness, b) abundance and c) temporal diversity variation in forest islands at the Espinhaço Range, southeastern Brazil, with and without cattle presence.



Supplementary figure 4. Plots comparing the samplings over time (rainy season of 2014, 2015, 2018, and 2020) where the forest islands are plotted using the species losses and gains computed from incidence data of herbivorous insects present in understory (left) and canopy (right) strata. The green line indicates gains equal losses. The red line was drawn parallel to the green line (i.e., with slope = 1) and passing through the centroid of the points. Its position below the green line indicates that, on average, species losses dominated gains from Time 1 to Time 2 (and vice-versa). Circles indicate dominance of losses, while squares indicate dominance of gains or equal contribution of both components in each forest island. Circle and square sizes are scaled to their values.



Supplementary figure 5. Boxplots of herbivorous insect species a) gains and b) losses in forest islands at the Espinhaço Range, southeastern Brazil, with and without fire incidence.



Supplementary figure 6. Boxplots of herbivorous insect species a) gains and b) losses in forest islands at the Espinhaço Range, southeastern Brazil, with and without cattle presence.

Final conclusions and perspectives

The importance of forest-grassland mosaics in tropical mountains is undeniable. In addition to all that has been pointed out about the *Capões de Mata* system, we must consider the possibility that they function as a faithful model representing the fragmented landscapes of the future. As they are ancient natural forest islands, the *Capões de Mata* are a good example of how the environments that are being anthropically fragmented today could work in the future. Thus, monitoring these environments as well as their associated biodiversity can be an advantageous strategy for the development of environmental and conservation programs through the assessment of biodiversity change. Besides, in addition to the increasing threats that this system has been facing, it is worth mentioning the presence of invasive exotic species resulting from the crossing of wild boar with pigs, locally called “javaporcos” (personal communication with ICMBio employees). Together with the great pressure of climate change, this exotic fauna can accelerate the loss of biodiversity of this entire highly threatened system, mainly due to the habit of wallowing the soil and plant roots in search of food, causing loss of nutrients, leaching, and reduction of vegetation cover, diversity of herbs and shrubs (Cuevas et al., 2012). The impact can also extend to the exposure and homogenization of the seed bank structure (Webber et al., 2010; Bueno et al., 2011), decline in water quality and decrease in food resources through competition with native herbivores and predation of small wild animals (Rosa et al., 2016; 2018). Therefore, we suggest that priority measures be taken to control the population of this invasive fauna in the *Capões de Mata*, where the local community can be placed co-responsible for the control of this species since it has no natural predators and high reproductive rates (Long et al., 2003).

In this thesis, we showed in the first chapter that both spatial and temporal factors have mixed contributions to herbivorous insects’ diversity patterns and distribution. We found that the greatest change in the composition of these species was mainly due to seasonal variations in climatic characteristics, which may have indirectly contributed to the understory being the most diverse and stable stratum compared to the canopy. In the second chapter, we highlighted the complexity of the outcomes of disturbance by fire and large grazers in the study system, emphasizing fire as a major threat but also surprisingly indicating a potential benefit of cattle grazing in the protection of the fire-sensitive forest islands. In the third and final chapter, we evaluated the influence of these both disturbances, along with local properties of the forest islands, on the spatial distribution

of herbivorous insects. We evidenced fire as the only variable influencing the stability of herbivorous insects and the canopy cover variation as the only variable explaining colonization and extirpation processes. The consistent differences in the beta diversity of herbivorous insects associated with both understory and canopy of the *Capões de Mata* suggest that these communities may operate at different scales, where again we showed that the understory is more diverse and stable than the canopy.

The ecological patterns presented here can contribute significantly to the establishment of priorities and guidelines that support informed decision-making policy toward the sustainable use of tropical forest-grassland mosaics. Further, the knowledge of variations in herbivorous insect species diversity and composition can define essential parameters for the effective conservation of ecosystems and environmental services of tropical mountains. It can also be useful to suggest important areas for conservation and maintenance of diversity, which are still based on few criteria related to the distribution of insects through local and landscape changes and those generated by anthropic disturbances. In a constantly changing world, long-term studies that include a regional pool of species, encompassing other regions of Serra do Espinhaço, will help us to better track how natural history and factors related to global changes affect natural ecosystems.

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Appendix I

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Spatiotemporal Distribution of Herbivorous Insects Along Always-Green Mountaintop Forest Islands

Juliana Kuchenbecker^{1*}, Luiz Eduardo Macedo-Reis^{1,2}, Marcilio Fagundes³ and Frederico S. Neves^{1,4}

¹ Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil, ² Maram Projetos Ambientais, Ipatinga, Brazil, ³ Departamento de Biologia Geral, Centro de Ciências Biológicas e da Saúde, Universidade Estadual de Montes Claros, Montes Claros, Brazil, ⁴ Departamento de Genética, Ecologia e Evolução, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil

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*Correspondence:

Juliana Kuchenbecker
jubelsario@gmail.com

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Insects make up the bulk of terrestrial diversity and about half of insect species are herbivores that have direct relationships with their host plants and are the basis of the entire food chain, on which wildlife and humanity depend. Some herbivorous insect traits, such as their spatio-temporal distribution, are especially relevant in the current scenario of global changes, which are more pronounced in high elevation areas, helping to improve the effectiveness of conservation actions. Here we evaluated the influence that different spatiotemporal scales have on three free-feeding herbivorous insect guilds (fluid-feeding, leaf-chewing, and xylophagous insects) in montane forest islands immersed in a grassland-dominated matrix (*campo rupestre*). We assessed whether species turnover or nestedness was the main component determining both spatial and temporal species composition variation (β -diversity) of the herbivorous insect community. We also checked the temporal effect on herbivorous insect guilds composition between vertical strata. We sampled herbivorous insects during two summers and two winters in 14 forest islands of different sizes and shapes in a natural mountainous fragment located in southeastern Brazil. A total of 6597 herbivorous insects representing 557 morphospecies were sampled, 290 of which were fluid-feeding, 147 leaf-chewing and 120 xylophagous insects. We found a main contribution of time scale in the organization of the herbivorous insect composition sampled in this study, mainly by turnover, with small differences among guilds. Additionally, we could see that climate determined the local variation of species, corroborating that we have a highly variable always-green system over space and time where the understory community varies less in comparison to the canopy community. Our findings suggest that long-term ecological research on herbivorous community structure in relation to climatic variation is a key element for future investigations, which can be decisive for the conservation

Appendix II

Article published in the special volume of PELD–CRSC Newsletter - December 2021 edition

Kuchenbecker, J., Neves, F. S. 2021. Insetos herbívoros nos capões. In: Fernandes, G. W., Gélvez-Zúñiga I., Camarota, F., Siqueira, W. K. Warming 6:7-8.

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Warming

Uma Newsletter da PELO - CRSC

5. Insetos herbívoros nos capões



Capões. Foto: Paulo Ricardo Siqueira

As ilhas despertam o fascínio dos seres humanos há milênios, mas foi na década de 60 que elas receberam seu devido reconhecimento com o surgimento da Teoria da Biogeografia de Ilhas de Robert MacArthur e Edward O. Wilson. Essa Teoria serviu de base e estímulo para a compreensão dos processos que determinam a distribuição espacial de toda a diversidade biológica e vem sendo amplamente usada para assimilar e interpretar a dinâmica da biodiversidade de habitats terrestres fragmentados. Embora áreas fragmentadas pelo homem sejam amplamente estudadas, poucas pesquisas foram realizadas em fragmentos florestais naturais incorporados em uma paisagem adjacente mais aberta. Esses paisagens terrestres naturalmente fragmentadas são excepcionalmente valiosas para nós pois nos permite estudar como as espécies se comportam e como estão distribuídas sem precisarmos levar em consideração quaisquer prejuízos relacionados à perda de habitat causada pelo

ser humano. Neste sentido, os Capões de Mata da Serra da Espinhaço são ilhas de Mata Atlântica imensas no campo rupestre e representam ótimos modelos para testarmos hipóteses ecológicas, já que possuem dimensões reduzidas, diferentes graus de isolamento e fronteiras bem definidas.

São poucos os grupos de organismos que possuem dados coletados nos Capões de Mata. Grande parte do conhecimento sobre a fauna de invertebrados dos Capões associados aos campos rupestres vem dos Projetos Ecológicos de Longa Duração (PELD) na Serra do Cipó, Minas Gerais (CRSC/CNPq). Nestes projetos, os insetos dominam como o objeto de estudo mais frequente. Afinal de contas, são interessantes organismos para se estudar. Além de responderem rapidamente às modificações do ambiente, os insetos são coletados facilmente, tem curto tempo de geração e são normalmente muito abundantes. Particularmente, os insetos herbívoros representam gran-

de parte da abundância total de insetos, vivendo entre as espécies de plantas em busca de recursos alimentares. Estudar sua distribuição e padrões de diversidade é fundamental para entendermos como a biodiversidade global é formada. Entretanto, ainda existe uma grande lacuna em estudos ecológicos e sobre conservação.

Os insetos herbívoros amostrados nos Capões de Mata entre os anos de 2014 e 2015 registraram 6597 indivíduos. Destes, levando em consideração a forma que se alimentam da planta, aproximadamente 51% foram representados por insetos sugadores de seiva, 27% por mastigadores de folhas e 22% por brocadores de caules. Um grande número de espécies raras foi encontrado para esses três grupos alimentares, compreendendo aproximadamente 44% de toda a amostragem. Similarmente, foram encontradas muitas espécies únicas. Por exemplo, de todos os indivíduos amostrados, aproximadamente 60% eram exclusivos da sub-bosque, enquanto



Warming



Reuniões da família Camanducidae. Foto: Hugo Nêlson



Bananas em Vilhena. Foto: Luis Macedo Roca



Hemiplernus ist familia *Lysianidae*. Foto: Adrian Kucharski

12% eram exclusivos da copa das árvores. O que mais influenciou a diversidade de insetos herbívoros encontrada foi a mudança de espécies entre as ilhas florestais, o que indica que cada Capão de Mato deve ter uma comunidade única de insetos herbívoros. Nessa perspectiva, estes ambientes têm grande valor de conservação para muitas espécies, servindo como locais refúgio em uma paisagem fragmentada contendo uma diversidade inestimável de espécies. A presença de cada espécie em um Capão de Mato pode representar um amostra das espécies que vivem nas florestas contíguas adjacentes ou mesmo nas áreas abertas circunvizinhas, que se dispersaram para as novas florestas. Isso pode explicar parcialmente as altas taxas de espécies raras encontradas. Adicionalmente, os diásporos em partes a diversidade de insetos herbívoros para cada grupo alimentar, pensamos que o tempo (i.e., o passar das estações) contribuiu mais para a diversidade total de insetos herbívoros que características da paisagem, como a estratificação vertical (distribuição dos organismos ao longo do plano vertical da floresta) ou a distância entre os Capões de Mato. Assim, apesar de ser um sistema sempre verde, a sazonalidade climática destes Capões de Mato é o que mais impulsiona e contribui para a diversidade e diferenças na composição de espécies de insetos herbívoros.

Uma vez que os Capões de Mata estão localizados em uma altitude mais elevada com maior propensão a serem afetados por mudanças climáticas, o monitoramento da dinâmica espacial e temporal das insetos herbívoros nestes ambientes pode ser bastante útil para a interpretação de padrões de diversidade de espécies em um mundo cada vez mais dominado por paisagens modificadas pelo homem. Ademais, a importância destes ambientes vai muito além. Podemos considerar os Capões de Mata como reservatórios da biodiversidade da floresta obrigando grande número de espécies que outono estariam condenadas a desaparecer. Se assermos

gerenciar e conservar a diversidade biológica de maneira sustentável, apoiar e manter os estudos de longa duração nestes sistemas certamente terá um grande avanço na nossa compreensão a respeito das comunidades associadas a sistemas naturalmente insulares. Temos em mãos a respeito da diversidade de insetos herbívoros ao longo de gradientes de heterogeneidade ambiental e de pressões antrópicas é definitivamente uma estratégia super vantajosa para o desenvolvimento de programas de conservação e monitoramento de ambientes.



Baccharis monnina L. Foto: Luiz Adriano Reis

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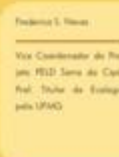
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Come on

Eisnerbecker, J., Neves, F. S. 2021. Insetos hibernos nos copões. In: Fernandes, G. W., Gálvez-Zúñiga I., Camarero, F., Siqueira, W. K. Warming 6.7-8. <https://doi.org/10.6084/m9.figshare.17554991>

Appendix III

Text about the *Capões de Mata* published with the assistance of the candidate on the conservation website: Bocaina Biology of Conservation

<https://biologiadaconservacao.com.br/cienciaemacao-capoes-de-mata>

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Um sistema florestal raro e ameaçado



JULIANA KUCHENBECKER

Bióloga - Mestre em Ciências Biológicas pela Unimontes e Doutoranda em Ecologia, Conservação e Manejo da Vida Silvestre pela UFMG. Tem atuação na Comunicação da Ciência e na Ecologia de Comunidades com ênfase em insetos herbívoros.



LUCAS PERILLO

Biólogo - Mestre e Doutor em Ecologia, Conservação e Manejo da Vida Silvestre pela UFMG. Tem atuação na Comunicação da Ciência e na Ecologia de Comunidades com ênfase em insetos.

Os capões de mata da Cadeia do Espinhaço

Antes de abordarmos os capões de mata, não podemos deixar de falar da grandiosa Cadeia do Espinhaço na qual eles estão inseridos. Essa formação montanhosa é super importante devido a sua alta biodiversidade e endemismo (espécies vegetais e animais que só ocorrem nela). Ela se estende por 1200km desde o norte da Bahia até o sul de Minas Gerais, agindo como uma importante barreira que divide 2 dos nossos maiores biomas: O Cerrado (formação campestre) e a Mata Atlântica (formação florestal). Espécies desses dois tipos de formação vegetal estão em constante luta pela sobrevivência. Em um determinado espaço, dependendo da temperatura, umidade e componentes do solo, por exemplo, um dos dois tipos de bioma se torna vencedor! Mesmo que não em definitivo, já que essas condições podem variar ao longo do tempo e podem ser afetadas pela ação do homem.

Veja mais:



PAPAGAIO DE PRIMATA

Papagaio de Primata, seu podcast sobre assuntos ambientais

<https://biologiadaconservacao.com.br/cienciaemacao-capoes-de-mata>



Vídeo 1: Projetos ecológicos nos capões de Mata. Conheça um pouco mais sobre os capões de mata, ilhas de vegetação que formam um arquipélago florestal no meio do campo rupestre <https://www.youtube.com/watch?v=J7rH6cQUda>

Acima dos 900m de altitude na região da Cadeia do Espinhaço há a prevalência de uma matriz campestre denominada campo rupestre, dentro da qual estão os nossos preciosos Capões de Mata. Ao imaginarmos ilhas, logo vem à mente imagens de pequenos pedaços de terra circundados por água. Bom, no caso dos Capões não é tão diferente assim! Os Capões de Mata só não são cercados por água mas são ilhas florestais associadas às áreas montanhosas do leste do Brasil, ocorrendo acima de 1.200 metros de altitude e envoltos por matrizes campestres. Um dos mecanismos para a manutenção dos Capões de Mata é a influência de uma altíssima umidade, característica das zonas de cume no alto das serras.



Série Naturalistas - Um portal dedicado aos pioneiros das ciências naturais



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<https://www.youtube.com/watch?v=otfWBRVC4vA>

Ameaças ao frágil sistema florestal

Os capões de mata estão localizados em uma zona de tensão ecológica tendo, portanto, alta relevância biogeográfica e destacando-se como áreas prioritárias a conservação. As principais ameaças a este sistema são o pastoreio, a supressão vegetal para aproveitamento de madeira e o fogo. O gado presente nos arredores, por exemplo, entra nas ilhas florestais abrindo caminho para as espécies campestres, além de facilitar a entrada do fogo. As queimadas por sua vez, frequentemente de origem antrópica, são o nosso principal problema, pois causam uma diminuição nas dimensões dos Capões de Mata alterando sua dinâmica sucessional.



Formando as ilhas florestais

O estabelecimento dos Capões de Mata é especialmente dependente do clima e do solo para seu desenvolvimento. Dessa maneira, estas ilhas florestais são consideradas uma formação edafoclimática, onde a altitude, as condições locais e características físicas do solo, a exemplo da drenagem, são extremamente relevantes. A grande variação estrutural (altura, área basal) observada para os Capões de Mata pode estar relacionada à enorme variedade de condições ambientais associadas às montanhas, entre elas as condições edáficas e topográficas.

Para saber mais:

> Tese de doutorado de Marcel Coelho: Os Capões de Mata da Cadeia do Espinhaço: padrões e processos ecológicos - UFMG
<https://repositorio.ufmg.br/handle/1843/BUBD-9VZGWB>

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Appendix IV

Video produced and published by the candidate on the Youtube platform about the *Capões de Mata* as part of the Method and Scientific Communication class during the content production exercise.

<https://www.youtube.com/watch?v=J7rfH6cQUdo&t=19s>



The image shows a YouTube video player interface. At the top left is a circular profile picture of a woman with long brown hair wearing a blue shirt. To its right is the video title 'Capões de mata' in white text, followed by a vertical ellipsis menu icon. The video thumbnail shows a landscape with a grassy field, a line of trees, and a blue sky with clouds. A large red play button is centered over the thumbnail. Below the video player, the title 'Capões de mata' is repeated in white. Underneath are three statistics: '6' for 'Marcações "Gostei"', '79' for 'Visualizações', and '2020' for '3 de nov.'. A horizontal line separates these statistics from the text below. The text is in white on a black background and describes the video's content about forest islands in the Espinhaço range, followed by acknowledgments to Ricardo Solar, Lucas Perillo, and Heron Hilário.

Capões de mata

6
Marcações "Gostei"

79
Visualizações

2020
3 de nov.

Você sabia que, além das tradicionais ilhas oceânicas, existem ilhas florestais no alto das montanhas? Este vídeo informativo vem trazer um pouquinho dos capões de mata, ilhas florestais situadas ao longo da nossa grandiosa Cadeia do Espinhaço. Aqui vc vai ter a oportunidade de aprender sobre essas ilhas, entender a sua dinâmica, importância e algumas das principais ameaças a este sistema. Vem conhecer e nos ajudar na desafiadora missão de fazer este sistema ser visto e respeitado!

Agradecimentos especiais aos colegas que proporcionaram a maior parte das belíssimas imagens contidas nesta apresentação:
Ricardo Solar
Lucas Perillo
Heron Hilário

Appendix V

Video produced by Jandaia: Histórias Tropicais, in which the candidate gives a short interview about the *Capões de Mata* in order to publicize the project “Long-term Cascade Effects of Fire on Savanna Biodiversity in the Southern Hemisphere: Brazil and Namibia”.

<https://www.youtube.com/watch?v=XjUSc8IVcUQ>

Efeitos em Cascata de Longo Prazo do Fogo na Biodiversidade Savânica no Hemisfério Sul: Brasil e Namíbia

Cascading Long Term Effects of Fire on Savanna Biodiversity in the
Southern Hemisphere: Brazil and Namibia

Descrição



Efeitos em Cascata de Longo Prazo do Fogo na Biodiversidade Savânica no Hemisfério Sul

22

Marcações "Gostei"

242

Visualizações

5 de jul.

2022

Vídeo de divulgação do projeto "Efeitos em Cascata de Longo Prazo do Fogo na Biodiversidade Savânica no Hemisfério Sul: Brasil e Namíbia"

Roteiro: Fernando Goulart & Geraldo Wilson Fernandes

Produção: Fernando Goulart & Luiza Kot – Jandaia:

Histórias Tropicais

Trilha sonora: Fernando Goulart

Apoio: Bio-Bridge Initiative - Convention on Biodiversity (UNEP), Pesquisa Ecológica de Longa Duração PELD - CRSC, CNPq & FAPEMIG

Julho, 2022.