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Vegetation dynamics after fire in the Brazilian *Campo Rupestre*: Effects on native plant communities and flower harvesting

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ABSTRACT

We investigated the impact of both early and late fires on native plant communities of the C*ampo Rupestre* in the Sempre-Vivas National Park (PNSV, Brazil). Everlasting flower harvesters use late fires to stimulate flowering, while park managers have been implementing early fires to reduce flammable biomass and, therefore, the risk of wildfires. We aimed to explore the effects of fire on species composition, vegetation cover, and plant and flower stalks height to evaluate post-fire vegetation recovery, especially considering *Comanthera* species, which are highly valued by flower harvesters. The experimental design involved two areas (A1 and A2) in PNSV from May/2019 to January/2021. We installed eight 50 × 50 m plots in each area, being half submitted to experimental burnings and the other half unburned (control plots). A1 experienced early fire in May, and A2 a late fire in September. Initial phytosociological surveys revealed differences between A1 and A2, therefore, fire effects were treated separately for each area. In both A1 and A2, fire initially impacted species richness and abundance but the effect dissipated over time, with vegetation becoming similar to unburned plots. Fire also affected vegetation cover, which returned to its original condition within a year, influenced by seasonality and plant phenology. Plant communities experienced a temporary reduction in height (~4 cm) in the months following fire, and recovered in the subsequent rainy season. However, a tendency for smaller plants persisted, and the average height of flower stalks took almost two years to fully recover. In general, the late fire conducted in A2 led to a slower recovery trajectory. These findings indicate rapid post-fire biomass recovery and minimal impact on plant species composition, highlighting the resilience of C*ampo Rupestre* to single fires. Further studies are crucial to understand plant response to fires at different fire frequencies.

1. Introduction

Fire has been a fundamental driver for the evolution and maintenance of several ecosystems in the world (Bond and Keeley, 2005; Hardesty et al., 2005; Bowman et al., 2016), shaping landscapes and influencing biodiversity patterns. In fire-prone ecosystems, particularly tropical grasslands and savannas, fire harbors potential benefits for the vegetation (Pivello et al., 2021), favoring the cycling of organic matter, increasing the incidence of light and nutrients at ground level, and creating open spaces for the establishment of new individuals (Pivello and Coutinho, 1992; Wrobleski and Kauffman, 2003). Thus, the effects of fire on the environment can be positive or negative, depending on where, when, and how it occurs (Hardesty et al., 2005; Fidelis, 2020; Pivello et al., 2021). These effects are influenced by fire parameters such as intensity, frequency, and seasonality – which make up the fire regime – with different outcomes in the composition and diversity of plant communities (Pivello and Norton, 1996; Oliveras et al., 2013; Pivello et al., 2021).

In Brazil, periodical fires have significantly influenced the evolution and maintenance of the Cerrado vegetation (Simon et al., 2009; Pivello et al., 2021). Within this biome, the highest mountains (altitudes above 900 m) host unique rupestrian grassland complexes, regionally known as C*ampo Rupestre*. This vegetation is composed of mosaics of ancient, grassy-shrubby vegetation, characterized by high biodiversity,

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remarkable endemism and micro-site heterogeneity (Rapini et al., 2008; Silveira et al., 2016). These grasslands have established on quartzite, sandstone and ironstone formations, where soils are extremely poor, and are mainly distributed along the Serra do Espinhaço, in the states of Minas Gerais and Bahia (Silveira et al., 2016; Le Stradic et al., 2018). Wide altitudinal and latitudinal variation, different soil types, and diverse microclimates compose the heterogeneity of habitats in these environments, which have favored the great floristic richness and endemism rates (Rapini et al., 2008; Silveira et al., 2016). Therefore, *Campo Rupestre* is a highly heterogeneous environment, characterized by diverse microhabitats and significant biodiversity (Arruda et al., 2023; Caminha-Paiva et al., 2022)

Plants popularly known as "everlasting flowers" (*sempre-vivas*), which mainly belong to the Eriocaulaceae, Xyridaceae, Poaceae and Cyperaceae families (Giulietti et al., 1996), are considered symbols of the *Campo Rupestre*, due to the great diversity of endemic species in the region (Martins, 2019). The inflorescences of these plants, particularly those in the *Comanthera* genus (Eriocaulaceae), hold significant commercial value due to their ability to retain their shape and color even after being harvested and dehydrated; this is why they are referred to as “everlasting flowers”. They are commonly used in decoration and handicrafts (Giulietti et al., 1987; Martins, 2019). For commercial purposes, the height of floral stalks is an important characteristic for the selection of harvesting species (Bedê et al., 2018), although there are indications in the literature that shorter stalks would also be acceptable for handicrafts (Oliveira et al., 2015, 2014). In any case, commercialization is based on the dry weight of the raw material, therefore, the larger the structures, the greater the biomass, and consequently, the greater the flowers’ value. Additionally, inflorescences with longer stalks are easier to harvest, demanding less physical effort in the field.

Comanthera species are the most valued in the commercial ornamental plant trade, and the overexploitation of selected species – notably *Comanthera suberosa, C. brasiliana* and *C. magnifica*, along with the particulartly vulnerable *C. elegans* – has led them to be considered threatened with extinction (Bedê et al., 2018; Carmo et al., 2021). Several of these species naturally occur in the Sempre-Vivas National Park (PNSV), a fully protected federal reserve located in the state of Minas Gerais (BRASIL, 2002). Since 1931, everlasting flowers have been harvested within the PNSV and surroundings, with this activity evolving to an important income source for local peasants since the 1970′s, boosted by exports to the United States, Japan and some European countries (Giulietti et al., 1987; Costa et al., 2008). This has led harvesting to uncontrolled quantities, and without due consideration for seedling recruitment in the following year, causing the decline of some populations (Menezes and Giulietti, 2000; Martineli and Moraes, 2013). Furthermore, excessive harvesting may reduce seed availability for subsequent year seedling recruitment (Bedê et al., 2018). Inappropriate fire management, particularly when fires exhibit excessive intensity or frequency, could also contribute to the reduction of *Comanthera* populations (Gomes et al., 2020; Rodrigues and Fidelis, 2022). However, the primary impacts of harvesting and fire management remain uncertain.

Fire, both as a natural and human-induced disturbance, drives the ecological dynamics of the C*ampo Rupestre*, exerting significant influence on its composition and resilience (Le Stradic et al., 2018; Fernandes et al., 2021). While historically occurring as a natural element of these ecosystems, human activities have increasingly introduced fires, altering the frequency, intensity, and spatial patterns of fire events (Pivello et al., 2021; Diele-Viegas et al., 2022). This anthropogenic influence adds complexity to the role of fire, amplifying its impact on vegetation dynamics, nutrient cycling, and habitat heterogeneity (Salim et al., 2022). Consequently, the interplay between natural and human-induced fires in the C*ampo Rupestre* underscores the need for comprehensive understanding and management strategies to mitigate potential ecological disruptions, while fostering the conservation of these unique habitats (Giorgis et al., 2021). Fire is often applied by the harvesters of everlasting flowers to stimulate flowering of the plants (Neves et al., 2011; Figueira et al., 2016), usually at the end of the dry season (late fires), in September-October (Bedê et al., 2018). Managers of the PNSV have been applying controlled burnings at the beginning of the dry season (early fires), in May-June, with the purpose to reduce the combustible biomass and, therefore, the risk of uncontrolled fires spreading into fire-sensitive vegetation, such as riparian forests (Fidelis, 2020).

Although fire is employed by traditional communities to induce flowering and increase flower abundance, as well as by the management authorities of PNSV for biomass control as part of an initial effort to implement Integrated Fire Management (IFM), knowledge on the broader ecological effects of fire on the *Campo Rupestre* remain scarce compared to other ecosystems, where information has been summarized in reviews (Giorgis et al., 2021; Roces-Díaz et al., 2022). The specific responses of various species within this unique ecosystem remain poorly understood (Fernandes et al., 2021; Salim et al., 2022) and the current knowledge is primarily limited to the specific impacts on the germination and establishment of a few species, including *Comanthera elegans*. Given the outstanding biodiversity and endemism of *Campo Rupestre*, it is crucial to understand how fire affects these systems beyond immediate and observable effects, such as potentially driving plant community composition and influencing long-term ecosystem stability. While fire management practices aim to balance conservation and traditional land use, comprehensive research is needed to elucidate the complex responses of *Campo Rupestre* to fire, ensuring that such interventions support sustainable ecosystem management and biodiversity conservation.

Given the limited knowledge of the effects of fire on the plant communities in the *Campo Rupestre*, especially the gap related to fire effects according to the context in which it is used, this study aims to provide pioneering results that can contribute to a better understanding of how this vegetation responds to fire applied at different times. Such insights can in turn facilitate the design of more effective management and conservation strategies for these unique ecosystems. Thus, we aimed to investigate the effects of early and late fires on native plant communities in a *Campo Rupestre* area seeking to answer the following questions: a) What are the effects of fire on the species composition, horizontal structure (vegetation cover) and vertical structure (plant height) in this ecosystem? b) How does vegetation recover from the effects of fire over time since the burning? Furthermore, considering the potential importance of floral stalk height for the activities of local flower harvesters, especially for the genus *Comanthera*, we aimed to answer the question: c) How does exposure to fire alters the recovery of floral stalk height in everlasting flower species? We hypothesized that fire events would prompt significant alterations in vegetation composition and structure in the short-term following a fire, potentially resulting in decreased species diversity and variations in morphological traits due to phenotypical plasticity. More specifically, we anticipated notable responses to fire disturbance in the *Comanthera* species, particularly regarding flowering and vigor, potentially influencing observable changes in the community structure. We expected this effect to be mostly pronounced on floral stalks, given the conventional use of fire by everlasting flowers harvesters. We additionally expected distinct effects of early and late fires, as late fires are usually more intense and could produce higher impacts on plants.

2. Material and methods

2.1. Study sites

The study was carried out in the Sempre-Vivas National Park (PNSV), located in the southern portion of Serra do Espinhaço (17°44′11″ to 17°59′28″S and 43°35′50″ to 43°59′33″W), Minas Gerais, Brazil. The regional climate is mesothermal (Cwb according to the Köppen classification), with humid summers (October to March) and dry winters (April to September) (Loiola et al., 2023); average monthly rainfall and temperature are respectively 112.64 mm (annual average from 1200 to

1500 mm) and 21.0 °C (MMA, 2016). Soils are very acidic (pH between 4.0 and 4.5), chemically poor, with high levels of exchangeable aluminum, sandy and highly susceptible to erosion (Silveira et al., 2016; Loiola et al., 2023). The PNSV is included in the Cerrado Domain and comprises several vegetation forms: gallery forest, submontane semi-deciduous and dry forests, savanna, *vereda* (hygrophilous palm tree savanna), and many types of grasslands (MMA, 2016; Silveira et al., 2016). In the highest (above 900 m) and hilly relief, on lithic soil of quartzite origin, one can find the "rupestrian grassland complex", characterized as a mosaic of plant communities adapted to the local topography, substrate, and microclimate (MMA, 2016).

2.2. Experimental design and data sampling

The study was carried out in two areas traditionally used for collecting everlasting flowers within the PNSV: A1 = *Morro do Urubu* (18°55′26.5′′S and 43°45′90.1′′W) and A2 = *Morro do Galho* (17°55′77.6′′S and 43°48′50.0′′W) (Fig. 1). Both areas were intensely used for everlasting flower harvesting from the 1970s to 1990s, but we have no information about harvesting frequency. Since 2002, when PNSV was established, both areas have been randomly burned, in both early and late seasons (PNSV staff communication). For the experiments, A1 and A2 were divided into eight 50 × 50 m plots, four of which received fire treatment (Fire) and four were considered control (Control). Each plot received 10 subplots measuring 1 × 1 m, totaling 80 subplots in each area (sampling units) (Fig. 1).

Both areas display a characteristic low vegetation structure, composed of a variety of herbs, especially graminoid and rosette-form species, with only a few plants exceeding one meter in height. Woody individuals are scarce in both A1 and A2. The percentage of soil cover varies across the plots in both areas, ranging from places with bare soil to those densely covered by vegetation. In some locations, it is possible to observe rocky outcrops amidst the vegetation, especially in A1 (Fig. 2).

Each A1 and A2 experienced only one experimental burning. A1 was burned in May 2019, at early dry season (early fire), following the prescribed burning schedule implemented by PNSV staff to control the combustible material. In A2, the burning was carried out in September 2019, at the end of the dry season (late fire), as usually practiced by the everlasting flower harvesters. The burnings were carried out by trained personnel from the Chico Mendes Institute for Conservation and Biodiversity (ICMBio) and the PNSV fire brigade.

Vegetation data collection in both burned (Fire treatment) and unburned (Control treatment) plots began in May/2019 (only in A1), followed by September/2019, January and May/2020 and January/2021, for both A1 and A2. The September/2020 sampling could not be done due to restrictions imposed by the Covid-2019 pandemic. The parameters collected in A1 and A2 subplots are related to the post-fire recovery of plant communities: vegetation cover and height of the vegetative and reproductive structures. The ground cover of each species was estimated visually (percentage of the area occupied by each species) in each 1 m^2 sub-plot. Since some species may overlap at different heights, the total

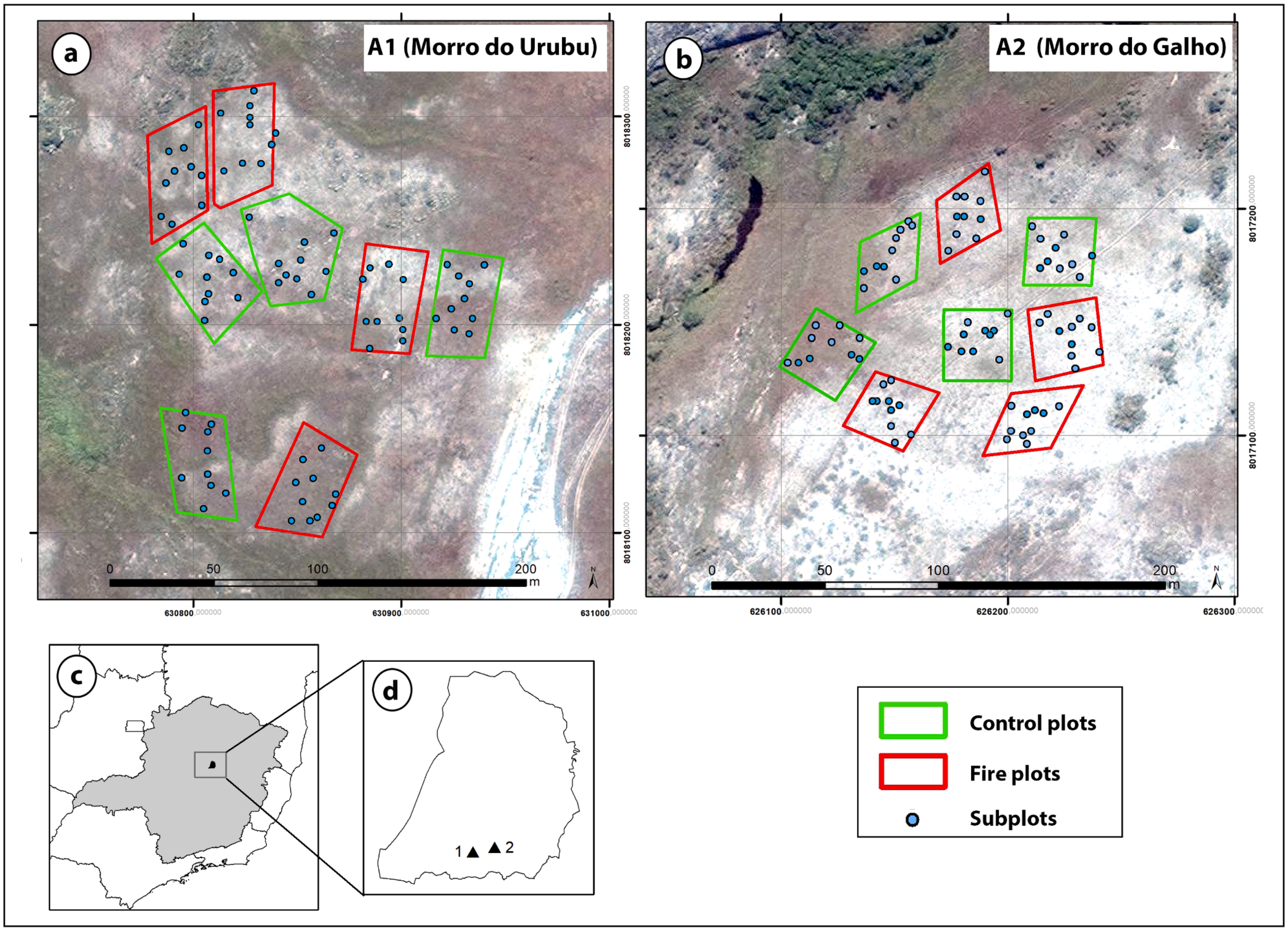

Fig. 1. Location of study areas and experimental plots. a = Fire and Control plots with subplots in Area 1 (Morro do Urubu); b = Fire and Control plots with subplots in Area 2 (Morro do Galho); c = Location of the Sempre Vivas National Park (PNSV) in Minas Gerais state, Brazil; d = Location of study areas (A1 and A2) within the PNSV. Maps designed by Simone Nunes Fonseca (ICMBio-Brazil).

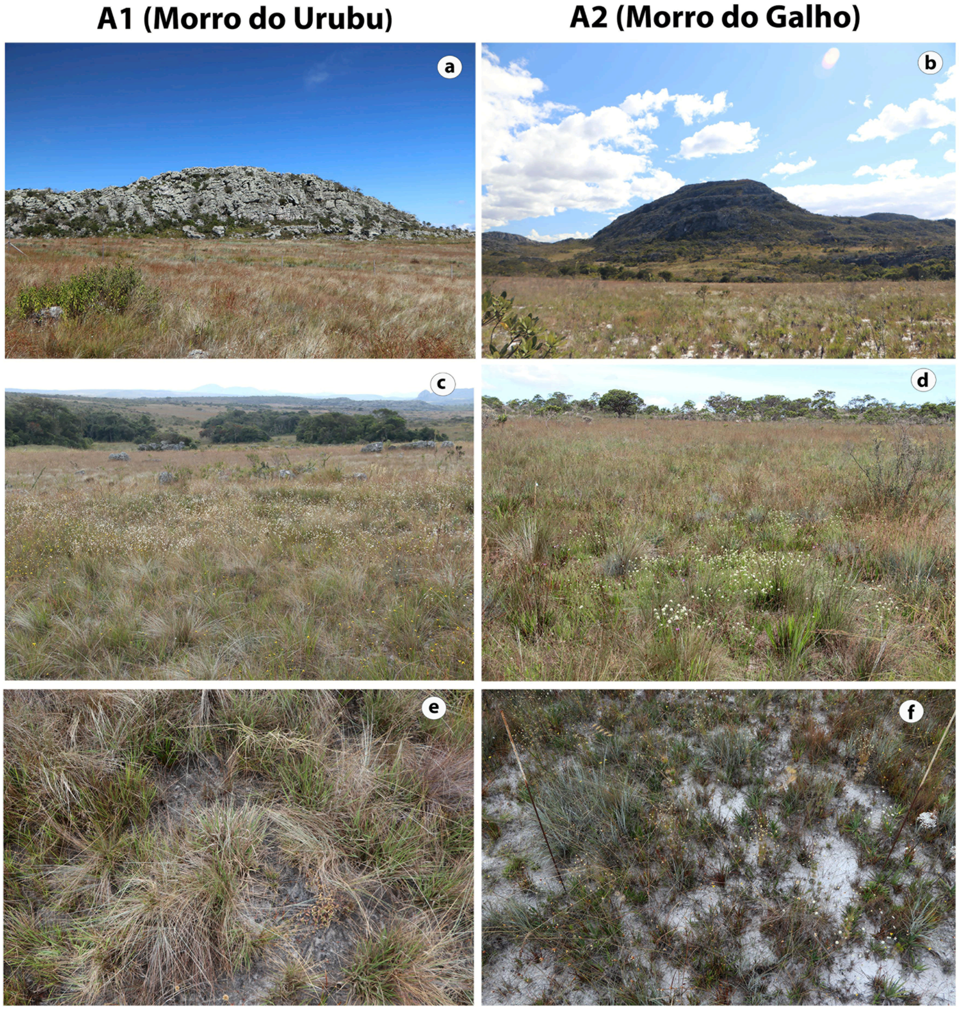

Fig. 2. Details of the vegetation physiognomy in the study areas, in the Sempre Vivas National Park (PNSV), Minas Gerais state, Brazil. a, c, and e: A1 (Morro do Urubu); b, d, and f: A2 (Morro do Galho).

sum of the occupancy percentages can be higher than 100 %. The maximum heights of the vegetative and reproductive structures of each species were measured *in loco*.

In all samplings (from May/2019 to January/2021), every species found in the 1 m^2 subplots was identified to the most detailed taxonomic level possible. Taxonomic identification followed Flora and Funga do Brasil (2024), and it was performed by specialists using identification keys and the infrastructure of the University of São Paulo herbarium. We calculated species diversity metrics for A1 and A2, represented by the Shannon-Weaver (H') and Simpson (D) indices, and Pielou's evenness (J), using the *diversity* function and J with the *specnumber* function from the *vegan* package in the R software (Oksanen et al., 2013; R Core Team, 2021).

The first floristic survey carried out before starting the fire experiments revealed differences in species composition between A1 and A2 (Figure S1). Due to this reason and the lack of replication of different times of fire, comparing the effects of fire according to the burning season (A1= early burning; A2= late burning) became unfeasible. Therefore, we evaluated the effects of fire on vegetation independently for A1 and A2, considering the plant community response according to the time elapsed since the fire event as the main parameter for comparisons.

2.3. *Statistical analyses*

The difference in plant community composition of both study sites and fire treatments over the sampling period (Set/2019 to Jan/2021) was tested using a permutational analysis of variance (PERMANOVA) based on 999 permutations in the *vegan* package of the R program (Oksanen et al., 2013). According to the observed significance, multiple comparison tests were performed using the *RVAdememoire* package (Hervé, 2020). We used a non-metric multidimensional scaling (NMDS) to observe the patterns of plant composition in communities according to post-fire treatments.

We used linear mixed models (LMM) to compare each response variable (vegetation cover, plant height and floral stalk height) as a function of the fire occurrence in each area and over time. We used the identification of the subplots as a random variable in each model to isolate temporal variation, since the repeated measurements occurred in the same subplots . For each response variable, we considered the total values (calculated per subplot), however we also built models including botanical family and botanical genus as explanatory variables, to understand at what taxonomic level the fire effect would have occurred and how long it lasted. Particularly for the genus *Comanthera*, we modeled the inflorescence height as a function of fire occurrence, the burning season (by considering A1 and A2), and temporal variation. We also included the identification of subplots and *Comanthera* species as random variables in the model. The response variables were square-root transformed to better fit the assumptions of normality of the residuals. All models were tested with Analysis of Variance considering the sum of squares of type 3, followed by significance tests of the marginal mean estimates, using respectively the *car* and *emmeans* packages of the R environment (Fox and Weisberg, 2011; Lenth, 2018).

3. Results

3.1. Fire effects on plant community composition

The floristic samplings (from May/2019 to January/2021) resulted in a total of 121 species belonging to 31 families. In A1, 101 species belonging to 28 families were identified, and in A2 we found 97 species belonging to 27 families (Table S1). The most abundant families were the same in both areas: Eriocaulaceae, Xyridaceae, Poaceae, Cyperaceae and Asteraceae, which showed strong dominance in the community. Fifteen of the 31 families found had only one species each (Table S1). Both areas showed high and similar species diversity according to the Shannon ($H'_{A1} = 2.47$; $H'_{A2} = 2.69$) and Simpson ($D_{A1} = 0.90$; $D_{A2} = 0.92$) indices and high equability ($J_{A1} = 0.99$; $J_{A2} = 0.99$).

The community composition (species richness and abundance) before starting the fire treatment was different between areas A1 and A2, but similar between the Control and Fire plots within each area (Table 1; Table S2). The occurrence of fire affected species composition in plots A1 and A2, but this effect dissipated over time (Table 1). The post-fire recovery dynamics in areas A1 and A2 exhibit distinct trajectories, preserving differences between the areas throughout the study period. However, there was a noticeable trend towards increasing similarity in vegetation composition between Fire and Control plots (Fig. 3; Table S2).

3.2. Fire effects on vegetation cover

The average percentage of plant cover was also different between A1 and A2 before the fire treatment ($\chi^2 = 16.642$; df= 1; $p < 0.001$) and over the time elapsed after fire ($\chi^2 = 35.096$; df= 3; $p < 0.001$). Within areas A1 and A2, the fire treatment differentiated the percentage of vegetation cover ($\chi^2 = 4.714$; df= 1; $p = 0.03$), but the greatest variation occurred over time ($\chi^2 = 18.114$; df=4; $p = 0.001$) (Table 2). In A1, four months after the burning and in the end of the dry season (Sept/2019), there was a reduction of approximately 9 % in the vegetation cover in the Control plots compared to the initial state (May/2019). After eight months (rainy season in Jan/2020), vegetation cover increased by 23 %, slightly exceeding the initial condition of vegetation cover (Fig. 4, Table S3-S4). In the Fire plots, four months after burning (Sept/2019, end of dry season), vegetation cover was reduced by 27 % compared to the initial condition. However, it gradually recovered over the following eight months (Jan/2020, rainy season), with approximately 20 % increases observed every four-month period. At the end of the experiment (Jan/2021), the Fire plots had reached values very close (around 95 %) of those of the Control plots. Therefore, the average vegetation cover values in Control and Fire plots were very close one year after the early fire (Fig. 4).

Table 1
Permutation analysis of variance (PERMANOVA) comparing the species cover composition of the two sampled areas in the Parque Nacional das Sempre-Vivas according to the fire occurrence and time after the burning. Significant effect ($p < 0.05$) in bold.

Effects	Df	Sum of squares	R^2	F values	*p* values
Area	1	2.3978	0.1861	17.8095	**<0.0001**
Fire occurence	1	0.3599	0.0279	2.6728	**0.0036**
Area: Fire occurence	1	0.2825	0.0219	2.0982	**0.0169**
Time after fire	4	1.6723	0.1298	3.1052	**<0.0001**
Area: Time after fire	3	0.5129	0.0398	1.2690	0.1192
Fire occurrence: Time after fire	4	0.2812	0.0218	0.5222	0.9996
Area: Fire occurence: Time after fire	3	0.1080	0.0084	0.2673	1.0000
Residuals	54	7.2703	0.5643		
Total	71	12.8847	1.0000		

In A2, vegetation cover in both the Control and Fire plots increased progressively and similarly until the end of the experiment. By the final two sampling dates, there was no significant difference in vegetation cover between the Control and Fire plots. The main difference in Fire plots – a decrease by 15 % in vegetation cover – was registered four months after fire (Jan/2020). After another four months (May/2020), vegetation cover was again similar between Control and Fire plots, although higher than at the starting of the experiment. Vegetation cover varied very little according to plant family (Figure S2) or genus (Figure S3), except for some months after the fire (Tables S5, S6 and S7; Fig. S2 and S3).

3.3. Plant and floral stalk heights according to fire treatments

The average height of the plant vegetative structures differed between sites and treatments over time ($\chi^2 = 35.447$; df=3; $p < 0.001$) (Table 2), with pronounced effects after the fire events (Fig. 5). Plant height differed among families and genera but varied little between Fire and Control conditions (Tables S8, S9 and S10). In certain families such as Asteraceae, Cyperaceae, Poaceae and Xyridaceae, plants exhibited greater heights at specific times in the absence of fire (Table S9). However, this effect was not observed at the genus level (Table S10), suggesting that the sum of the collective small increases across all genera within each family contributed to the observable effect at the family level. In September/2019, end of dry season and four months after the early fire treatment (A1, burned in May) the average height of plants was in 4.9 cm lower than before burning, while in A2 (late fire, burned in September), the reduction over the same period after fire, but in the rainy season (Jan/2020) was 2.3 cm. The recovery in the height of vegetative structures of plants occurred in less than eight months after fire in the early-burned subplots (A1), although, there was a tendency for the plants to become smaller overall (Fig. 5A). In A2, fire had a weaker effect on plant size, with an average reduction of only 1 cm. This effect was not statistically significant, even though the burned subplots still had a considerable reduction up to four months after the fire event (Jan/2020) (Fig. 5A).

The average height of the floral stalks also varied over time according to fire occurrence in both A1 and A2 (Fig. 5; $\chi^2 = 14.468$; df=3; $p = 0.002$), especially for the *Comanthera* species (Fig. 6; $\chi^2 = 10.802$; df=3; $p = 0.012$). However, most of the variance could be explained by the species' phenological responses to the rainfall season (see Time after fire, Table 2). Especially in the late-burned subplots (A2), there was a reduction in the average height of the floral stalks four months after fire, and full recovery was not achieved until Jan/2021.

4. Discussion

Our findings confirm our initial hypotheses about fire affecting plant communities in the *Campo Rupestre* and provide valuable insights into the dynamics of this vegetation under fire. However, contrary to our expectations, the fire treatments exert only short-term effects on species composition, with no significant effects observed beyond two years. Our study highlights the resilience of *Campo Rupestre* vegetation to isolated fires while emphasizing the importance of carefully considering both timing and intensity of fire events in management strategies.

The results also suggest that fire events occurring at short intervals could impede the full recovery of plant communities, as plants require a minimum period for adequate regeneration. This implies that management practices should allow for sufficient intervals between fires to ensure the proper community recovery. Moreover, our findings suggest that while the timing of fire events plays a significant role in vegetation

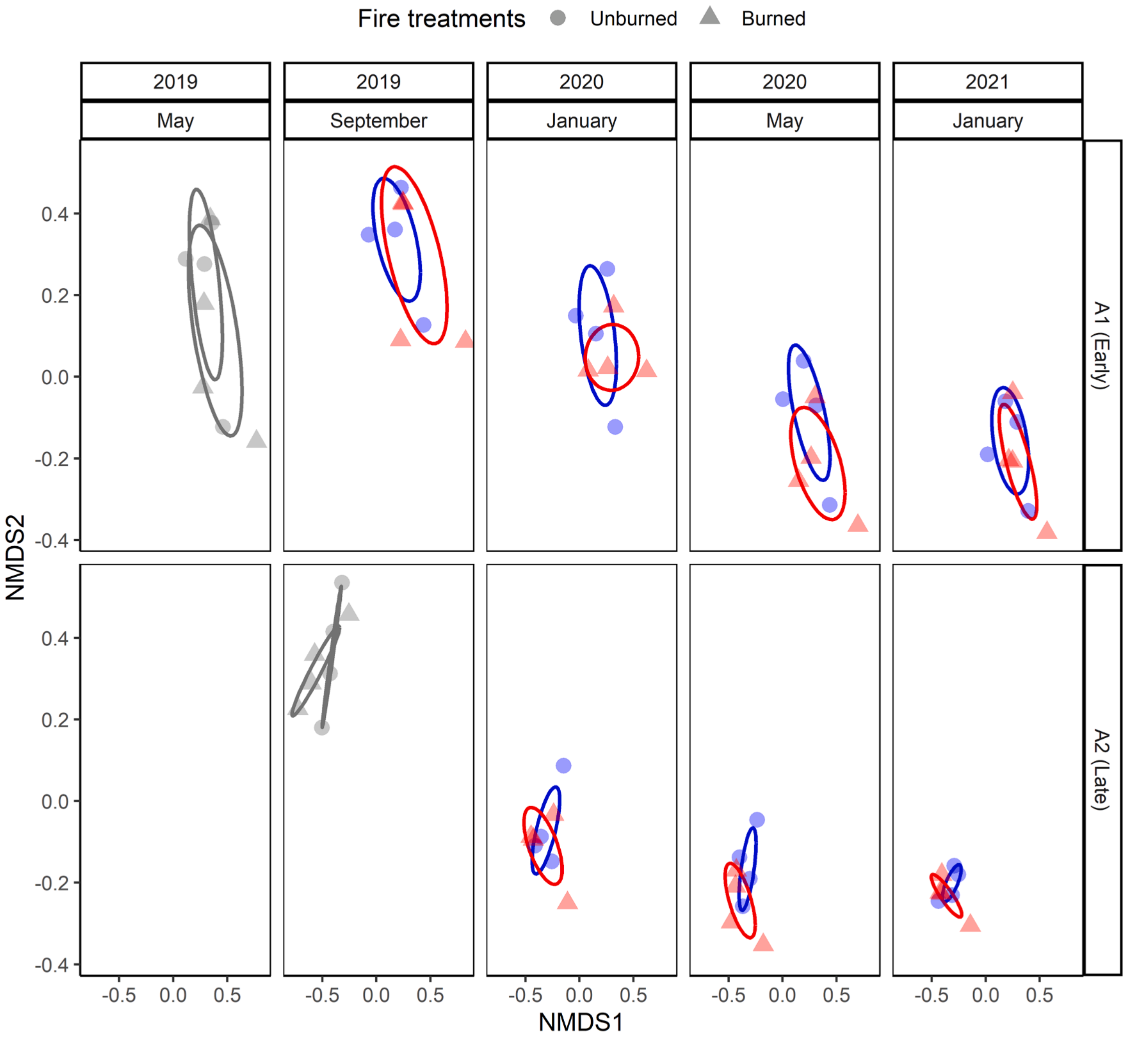

Fig. 3. Non-metric multidimensional scaling (NMDS - stress: 0.128) showing the differences in species composition in both A1 and A2 areas over time. Marks in blue represent unburned plots (Control), red are burned plots (Fire) and in gray, the respective plots before applying the experimental burning.

Table 2
Effect of fire occurrence, fire season (Early and Late), time after fire (month/year) and interactions, according to linear mixed models (LMM), on vegetation cover, plant height, height of floral stalks of all species, and height of *Comanthera* spp. floral stalks. Significant effect ($p < 0.05$) in bold.

		Vegetation cover		**Plant height**		**Height of floral stalks**		**Height of *Comanthera* floral stalks**	
Effects	df	χ^2	*p*-value	χ^2	*p*-value	χ^2	*p*-value	χ^2	*p*-value
(Intercept)	1	2168.02	**<0.001**	3021.40	**<0.001**	2683.53	<**0.001**	294.19	**<0.001**
Fire season	1	16.642	**<0.001**	4.627	**0.031**	0.253	0.615	0.016	0.898
Fire occurrence	1	4.714	**0.03**	30.579	**<0.001**	18.522	**<0.001**	0.894	0.344
Fire season: fire occurrence	1	0.063	0.802	22.706	**<0.001**	5.045	**0.025**	3.606	0.058
Time after fire	4	36.217	**<0.001**	11.981	**0.017**	47.91	**<0.001**	53.393	**<0.001**
Fire season: Time after fire	3	35.096	**<0.001**	5.132	0.162	10.358	**0.016**	1.924	0.588
Fire occurrence : Time after fire	4	18.114	**0.001**	47.409	**<0.001**	19.067	**0.001**	11.89	**0.018**
Fire season: Fire occurrence : Time after fire	3	1.492	0.684	35.448	**<0.001**	14.468	**0.002**	10.803	**0.013**

dynamics, the influence of phenology – referring to the seasonal changes in plant growth stages – cannot be overlooked in fire management approaches. Although fire has important effect on seedling responses in *Campo Rupestre* (Salomão and Hirle, 2019) the similar recovery of vegetation cover between Control and Fire treatments can be attributed to factors such as fluctuations in rainfall patterns (Silveira et al., 2016), local soil properties, or ecological mechanisms such as accumulated seed banks (Fernandes et al., 2021; Salim et al., 2022). In our study, a definite effect of seasonality was noted (Table 2).

Differences in the vegetation cover dynamics and recovery between areas subjected to early and late fire treatments were observed, but we cannot assume differential impacts of fire timing on vegetation recovery due to the initial heterogeneity of species composition between A1 and A2. Nonetheless, we emphasize that this is a topic that deserves further investigation. These findings highlight the need for tailored fire management strategies that account for the unique characteristics of each area, including species composition, growth rates, and environmental heterogeneity.

Although the fire treatment initially altered the species composition in A1 and A2, this effect did not persist over time after fire, and burned

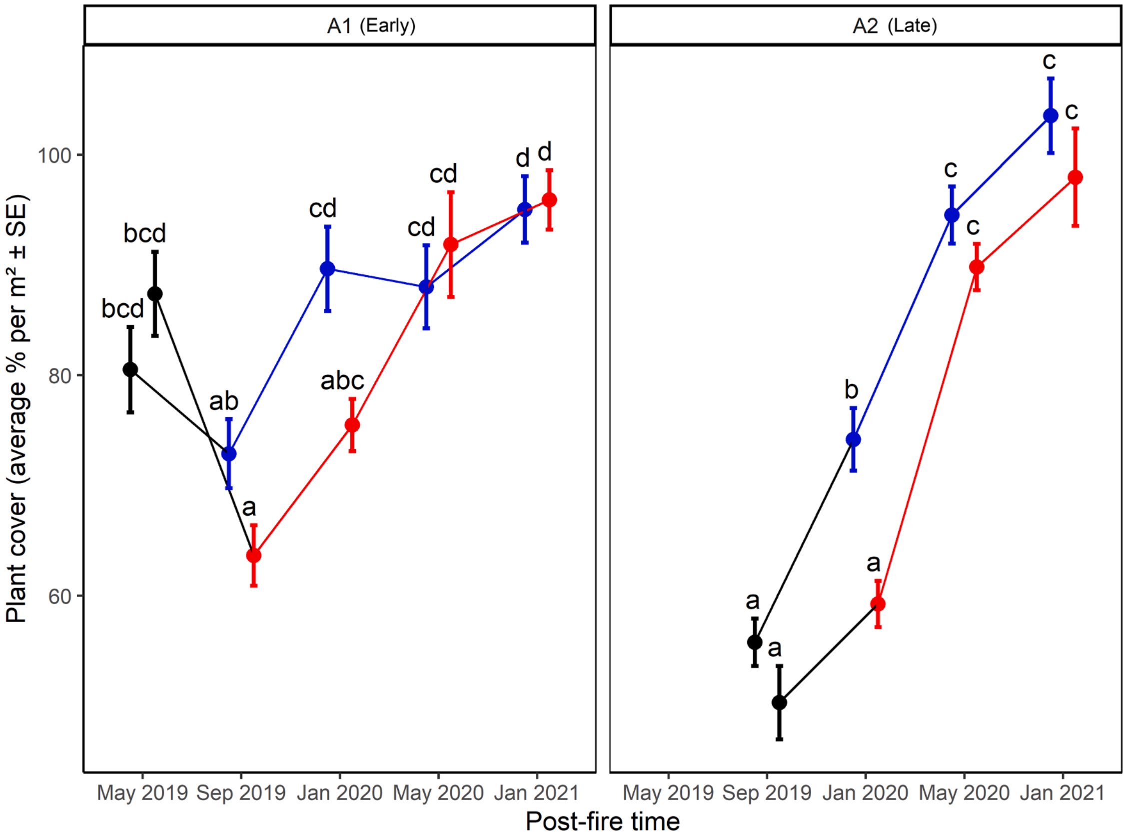

Fig. 4. Average vegetation cover per square meter in Area 1 and Area 2 according to burned (red) and unburned (blue) treatments over time. The black line indicates vegetation cover before applying the fire-treatment. (Vegetation cover values can exceed 100 % due to overlapping plants).

and unburned plant communities tended to closely resemble each other. This convergence of characteristics is influenced by seasonal responses corresponding to plant species life cycles, but also, such a trend can be supported by the fact that the most abundant families of plants in both areas were identical (Table S1). Previous studies (Araújo and Conceição, 2021; Le Stradic et al., 2018) have also shown abrupt changes in floristic composition one or two months after fire in *Campo Rupestre* which tended to return to the previous situation over time. In the same way as mentioned by Le Stradic et al. (2018), we agree that, over time, the effect of local heterogeneity can be more pronounced in shaping the recovery of floristic composition in the *Campo Rupestre* than the effects of fire, which makes the resilience of its vegetation to fire evident.

The dynamics of vegetation cover along time in both A1 and A2 was influenced by fire treatments as well as temporal factors, such as climate seasonality and plant species phenological patterns. In A1, where early burning was applied, vegetation cover initially decreased shortly after the fire but significantly recovered after eight months, reaching or surpassing values comparable to those in the Control plots. Conversely, in A2, the vegetation cover gradually increased over time in both Fire and Control plots, but there was a noticeable reduction trend in the burned plots, indicating the persistent effect of fire. On the other hand, the vegetation recovery was faster in A2, especially from the second to the third evaluation period post-fire. These results can be likely attributed to the greater abundance of graminoid species (Poaceae and Cyperaceae) compared to other plant families (mean grass cover: 6.98 %; mean cover of other families: 4.49 %; Tables S3-S4) in A2. Graminoids typically exhibit fast growth rates, which may explain the observed trend. In contrast, the abundance of *Vellozia* species was higher in A1, which are slow growing plants. Nevertheless, the recovery of vegetation cover in A1 reached and even exceeded pre-fire values, what did not happen in A2, even having more grasses. These contrasting patterns highlight the differential impacts of the fire timing on vegetation dynamics and may indicate amplified ecological disruptions associated with late fire events.

Furthermore, the observed recovery of the vegetation in the Fire plots also corroborates the resilience of these ecosystems to fire, as verified by other authors. Le Stradic et al. (2018) found that in two types of *Campo Rupestre* submitted to fire, vegetation cover returned to values similar to those before fire just five months after the fire occurrence. Neves and Conceição (2010) showed that native plants can rapidly recover spaces opened by fire, and this might be explained by morphological traits associated with resprouting strategies, such as lignotubers and xylopodial roots, underground stems and terminal buds protected in the center of tussock grasses (Kolbek and Alves, 2008; Neves et al., 2011; Oliveras et al., 2013). In addition, Joaquim et al. (2018) point out structural carbohydrates that can provide the recovery of aerial organs after environmental disturbances such as fire. Together with our results, these findings indicate that species from the *Campo Rupestre* are, indeed, highly resilient to fire.

The size of plant vegetative structures also varied over time and in response to fire treatment. Following the fire treatment, there was a noticeable reduction in the average height of vegetative plant structures in both A1 and A2, even though to varying degrees. While A1 experienced a more pronounced decrease in plants height followed by a recovery phase that approached pre-burning plants height, A2 showed a weaker effect on plants height. The dominance of *Vellozia* species in A1 – known for their caulescent rosettes and rapid height recovery from aerial apical buds – may have contributed to the initial faster increase in height observed in A1 compared to A2. While the dominance of *Vellozia* species in A1 may have contributed to the community height recovery, the delayed timing of fire events in A2 likely played a role in the slower height recovery observed there. Our findings suggest that early fires, even if less intense, can have stronger and extended effects on vegetation due to their timing just before the dry season. This period of additional stress slows down the recovery of vegetation height and structure. But in

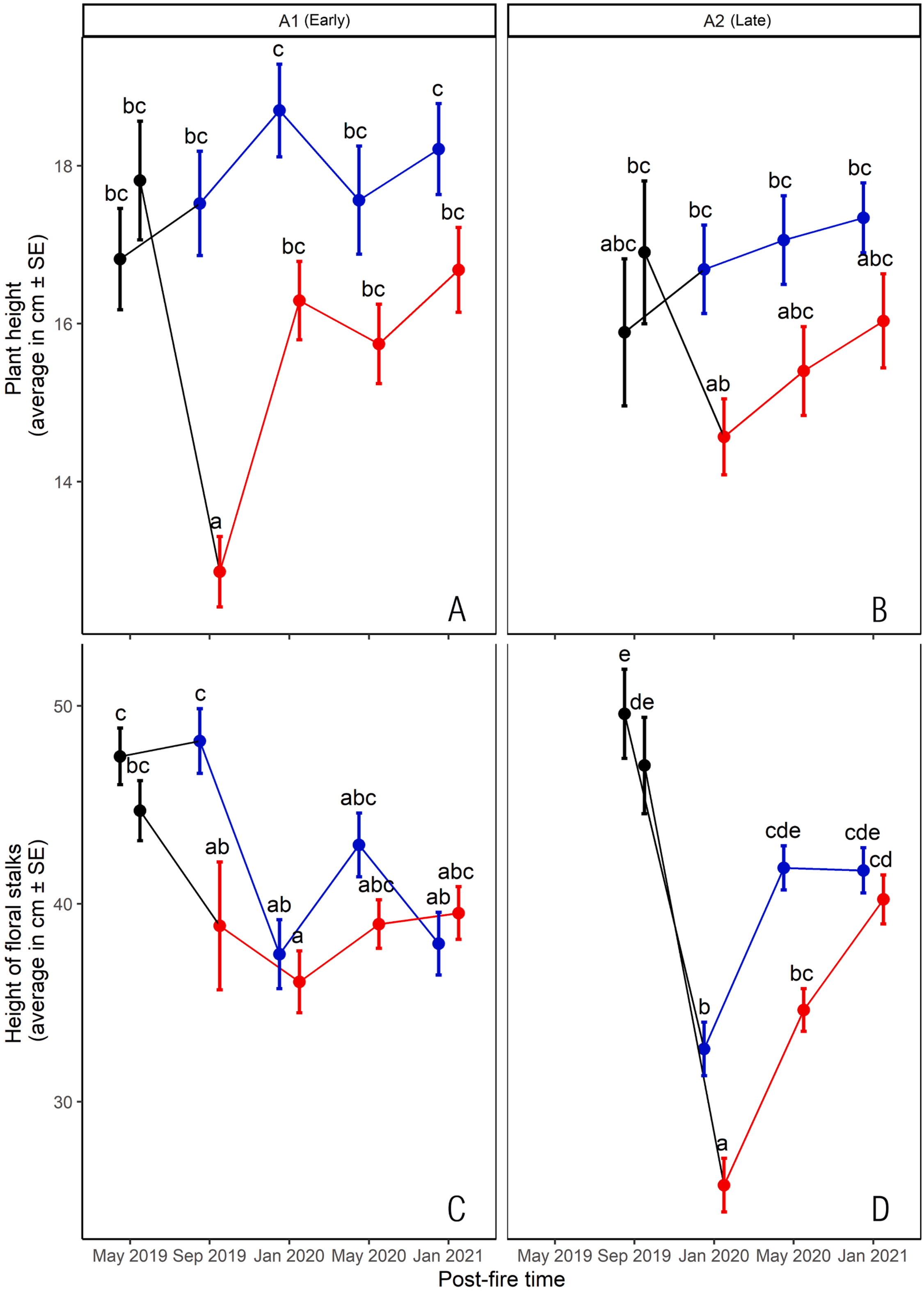

Fig. 5. Average plant height (A and B) and height of floral stalks (C and D), in Area 1 and Area 2 respectively, according to burned (red) and unburned (blue) treatments over time. The black line indicates respective heights before applying the fire-treatment.

both scenarios, a full recovery of plant height does not occur within one year after a fire, and a tendency for plants to remain smaller persisted.

It is thus important to consider that the varying impacts of fire timing on vegetation dynamics are not solely due to the presence of fire-adapted species but are also influenced by factors such as growth rates. These observations corroborate the discussion presented by previous studies (Araújo and Conceição, 2021; Le Stradic et al., 2018; Loiola et al., 2023; Oliveras et al., 2013), suggesting that the recovering patterns of vegetation after exposure to fire may be related to the floristic composition and plants life form, and evidence the importance of

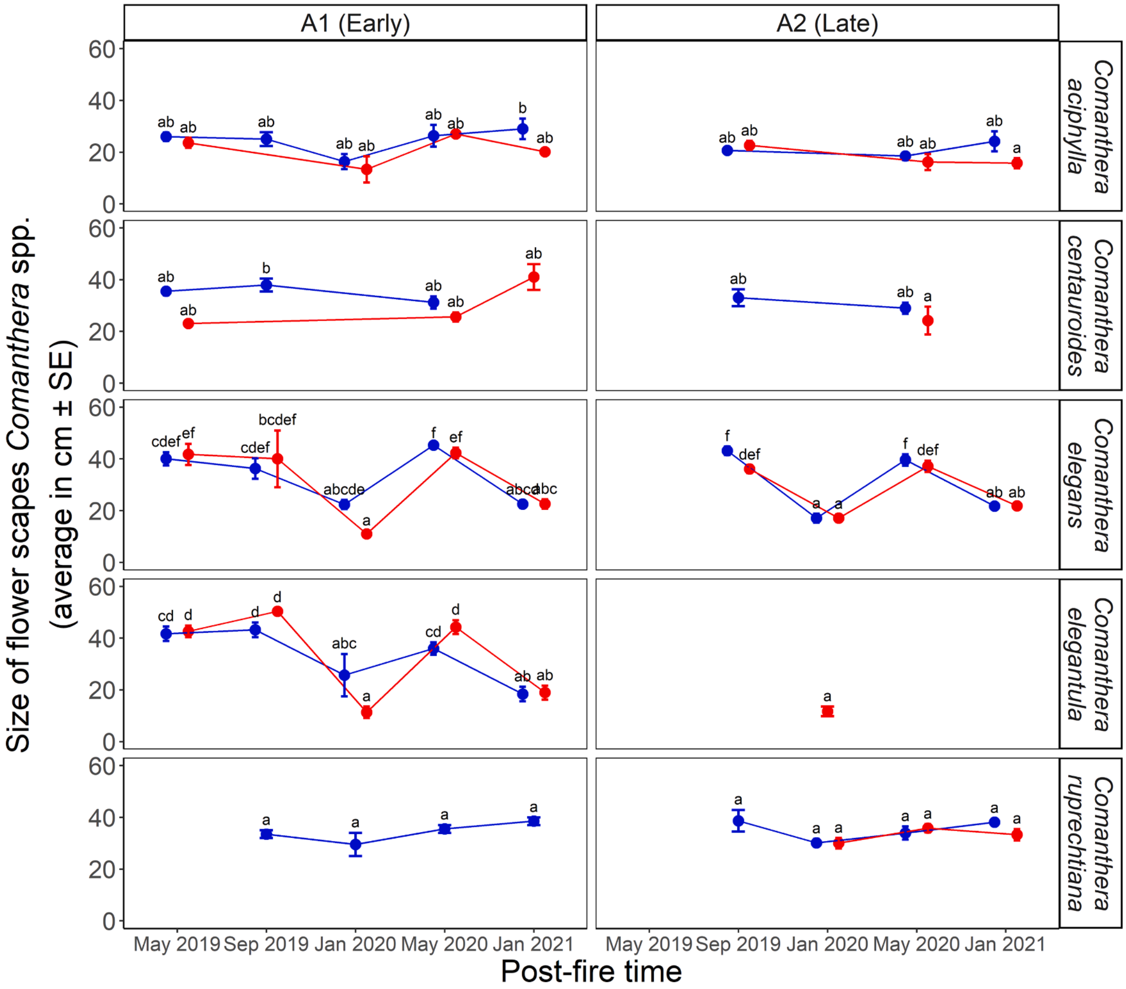

Fig. 6. Average height of *Comanthera* spp. floral stalks in Area 1 and Area 2 according to burned (red) and unburned (blue) treatments over time.

recognizing the composition of species and plant life forms of an area when planning controlled burnings.

Again, floral stalks height varied over time influenced by fire treatments and seasonality (phenology). In A2, there was a sharper decrease in the height of floral stalks after fire, but no complete recovery was observed over the study period. In A1, the recovery did happen. Particularly regarding some *Comanthera* species, our results indicate a similar trend of variations in response to fire and species phenology, however, these variations are mostly not statistically significant. Neves et al. (2011) observed fire effects on reproductive parameters in natural populations of Eriocaulaceae species, such as increase in the number of reproductive individuals (*Actinocephalus polyanthus, Comanthera elegantula* and *Syngonanthus nitens*), increase in the number of inflorescences per individual (*C. elegantula, Leiothrix crassifolia*) and increase in the number of seeds per flowerhead in a single studied species (*S. nitens*). However, the height of floral stalks was not considered in that study. As the *Comanthera* species are the most commercially valuable and some are already threatened with extinction, long-term studies looking at periodic burning at different times and frequencies (e.g. late versus early, annual, biennial) would be necessary to make a more accurate decision about the best fire regime to provide both a good and sustainable flower harvest.

The use of plant height as a proxy for biomass provides a critical perspective on the long-term impacts of controlled burns. As well as vegetation cover, height serves as an indicator of plant growth and overall vegetation productivity. Therefore, regarding vegetation cover and height dynamics following fire treatments, it becomes evident that late fires demand specific attention in the discussion of fire effects on plant communities in *Campos Rupestre*. Understanding these temporal dynamics is crucial for effective fire management in *Campo Rupestre* ecosystems.

5. Conclusion

Our findings are consistent with research conducted out in other *Campo Rupestre* sites, indicating fast biomass recovery after fire, and minimal significant changes in plant composition in response to fire. It appears that local heterogeneity plays a more significant role in driving floristic composition recovery in *Campo Rupestre* than fire effects. These observations suggest a high resilience of *Campo Rupestre* to single fires, although further studies are needed to assess their response to fires at varying frequencies. Regarding the dynamics of vegetation recovery after fire, our results demonstrate distinct trajectories in both areas (A1 and A2). The proportion of fast-growing graminoids and slow-growing *Vellozia* species in these areas suggests a slower recovery trajectory after a late fire. However, further experiments are necessary to confirm this observation conclusively. The time required for plants and floral stalks to regain their initial heights after a fire suggests that annual or biennial burnings may be too frequent for these ecosystems, allowing insufficient time for species to fully recover their growth potential, and not ensuring the ecosystems long-term sustainability. These results can also be of great value for planning the activities of flower harvesters, since the management based in constant fires could negatively impact the development of longer floral stalks, which are considered to be commercially more valuable.

Thinking about strategies for fire management in the *Campo Rupestre*, we advocate for a careful assessment of floristic composition, plant functional types and growth rates to plan controlled fires effectively, either for park managers or everlasting flower harvesters. Fire management practices can be optimized by simultaneously considering post-fire vegetation cover recovery, using vegetation cover and plant height as biomass indicators, and understanding the subtle differences between reproductive and vegetative structures. The complex dynamics of post-fire recovery evidences the need to tailor fire management strategies to the specific characteristics of each area, adopting an adaptive approach to ensure the ecological integrity and long-term sustainability of these unique ecosystems.

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CRediT authorship contribution statement

Gudryan J. Baronio: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Anna Carolina Gressler Bressan:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **Roberto Baptista Pereira Almeida:** Writing – review & editing, Writing – original draft, Methodology, Data curation. **Vânia Regina Pivello:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.flora.2024.152611.

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