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Prescribed burning in *Pinus cubensis*-dominated tropical natural forests: a myco-friendly fire-prevention tool

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Abstract

Aim of study: To evaluate the effects of two different prescribed burning strategies on ectomycorrhizal (ECM) fungal species in *Pinus cubensis*-dominated natural forest.

Area of study: Yateras Silvicultural Base Business Unit, Guantánamo, Cuba.

Materials and methods: In June 2015, six plots (20 × 50 m) were subjected to forward or back burning. Nine interval samplings (performed 1 week before and up to 120 days after prescribed burning) were undertaken to determine the total number of sporocarps and to evaluate the effect of fire on the soil.

Main results: Eight ECM species were collected from the study plots. *Suillus* sp. and *Amanita muscaria* started fruiting 15 and 60 days after the fire, respectively. *Boletus* sp., *Suillus brevipes, Suillus decipiens, Suillus* sp., *Amanita muscaria, Lactarius semisanguifluus, Scleroderma stellatum* and *Pisolithus arhizus* were found before and after prescribed burning. Sporocarp numbers showed an increasing trend after fire and significantly recovered 75 days after forward or back burning and were significantly higher 120 days after forward burning compared to unburned plots. The ECM fungal community in the heading fire and the backfire plots did not differ significantly. However, non-metric multidimensional scaling confirmed that ECM composition differed over time. According to a Mantel test, the sampling time after prescribed burning accounted for 64% of the variation in ECM composition, followed by edaphic factors (26%) such as organic matter and Na.

Research highlights: This preliminary study suggests that low-intensity prescribed burning does not have a negative effect on ECM fungal dynamics in humid tropical forests.

Additional key words: mushrooms; mycorrhizal fungi; forest ecology; fire ecology; Cuba

Abbreviations used: ECM (ectomycorrhizal); PB (prescribed burning); PBH (prescribed burning that act as a heading fire); PBB (prescribed burning that act as a backfire).

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Introduction

Fungi are increasingly recognized as important drivers of terrestrial ecosystem processes (Mohan *et al.,* 2014) and the high ecological importance of forests is in part due to the paramount roles played by fungi (Crabtree *et al.,* 2010). Mycorrhizal fungi are required for the survival and growth of some forest trees because they can extend the root exploration area beyond the rhizosphere through their hyphal networks (Smith & Read, 2008). Mycorrhizal fungi are therefore able to increase their host's resistance to abiotic stresses by enhancing water uptake and the mobilization, uptake, and translocation of nutrients in forest soils and, hence, can influence tree productivity (Van Der Heijden *et al.,* 2008; Pietras *et al.,* 2013). In addition, these root-associated beneficial symbionts are expected to improve the ability of their host trees to adapt to stressors associated with climate change (van der Linde *et al.,* 2018). They can also induce the aggregation of soil particles, improving soil aeration and porosity (Ryan & Kirkegaard, 2012). Other fungal species behave as saprophytes and are responsible for the decomposition of organic materials and, thus, the nutrient recycling (Ferris *et al.,* 2000). Beyond the importance of their ecological functions, edible fungi have also become a strategic component of forest management because of their economic value. During the past decade, there has been an increasing demand for edible forest fungi (Oria-De-Rueda *et al.,* 2008). Indeed, in some cases, mushrooms are becoming an important source of rural income (Boa, 2004; Abate, 2008).

Forest fires are one of the main factors driving the degradation of forest resources and affect most organisms (Dahlberg *et al.,* 2001; Bastias *et al.,* 2006; Rincón & Pueyo, 2010). Investigating the effects of fire on ecosystem functioning is currently a high priority, especially because of the increased wildfire risk associated with climate change (Westerling *et al.,* 2006; Pechony & Shindell, 2010). Fire can originate changes in the species composition of plant communities (Parks *et al.,* 2016). In addition, it may alter the soil properties and reduce microbial activity, causing changes in the availability of nutrients deep in the soil layer and directly influencing vegetation recovery (Reverchon *et al.,* 2010; Hernández-Rodríguez *et al.,* 2013; Parks *et al.,* 2016). Fire also affects forest fungal communities, particularly mycorrhizal fungi, due to the increase in soil temperature, the combustion of the organic layer, the deposition of ash, and the soil surface runoff (Cairney & Bastias, 2007). Furthermore, fire originates the loss of vegetation and, hence, a lack of colonizable roots, disrupting the continuity of the mycorrhizal interaction and affecting the life cycle of ectomycorrhizal (ECM) fungi. Indeed, Holden *et al.* (2013) concluded that ECM fungi are more sensitive to fire disturbance than other fungal guilds. However, ECM fungi also exhibit a wide spectrum of functional diversity, with underlying vegetative (Agerer, 2001), enzymatic (Courty *et al.,* 2010), and reproductive attributes (e.g., the production of fire-resistant propagules such as sclerotia as pointed out by Buscardo *et al.* (2010) who stated that such fungi are able to respond to fire at a species level). Overall, fire alters the specific composition and structure of ECM fungal communities (Dahlberg *et al.,* 2001; Bastias *et al.,* 2006; Cairney & Bastias, 2007; Rincón & Pueyo, 2010), which require many years to return to pre-fire conditions (Kutorga *et al.,* 2012; Kennedy *et al.,* 2014; Parks *et al.,* 2016). However, some fungi respond positively to fire treatments (Fritze *et al.,* 1993; Visser, 1995; Baar *et al.,* 1999; Kipfer *et al.,* 2011), fruiting abundantly soon after a fire (Wicklow & Hirschfield, 1979).

Although the effects of forest fires on fungal communities in different ecosystems have been reported (Martín-Pinto *et al.,* 2006; Gassibe *et al.,* 2011; Mediavilla *et al.,* 2014; Dejene *et al.,* 2017), little is known about how prescribed burning affects fungal populations in general (Dooley & Treseder, 2012). Prescribed burning, which is the planned use of fire under suitable environmental conditions to meet clear management objectives (Wade, 1989), is used as a tool to reduce the fuel load in forest systems, or as part of habitat management, or ecological restoration (Fontúrbel *et al.,* 2016; Reazin *et al.,* 2016). Prescribed burning is usually applied at low intensity and severity and, unlike most high-intensity wildfires, generally does not have a significant impact on fungal communities (*e.g.* Vázquez-Veloso *et al.,* 2022). Nevertheless, fungal communities could still be affected by these low-intensity fires owing to changes in the forest ecosystem balance (Bastias *et al.,* 2006). Thus, the subsequent structure of fungal communities might be affected, mainly driven by the dynamics of post-fire plant communities (Cairney & Bastias, 2007), which can be observed even after low-intensity prescribed burning. Several of these effects may be related to the soil temperatures that are reached during fires, decreases in carbon (C) and nitrogen (N) content, changes in nutrient and substrate availability, variations in soil and organic layer properties, and changes in organic matter (OM) quality (Fontúrbel *et al.,* 2016).

In Cuba, the use of fire is widely accepted as an agricultural management tool (Ramos, 2010). However, negligence while carrying out this activity frequently causes forest fires in natural and plantation forests every year (Ramos, 2010). Although prescribed burning is a widely used fuel management tool in some regions of the world (e.g., the USA, the Mediterranean Basin, and Australia), in tropical forests, and particularly in Cuba, this tool has barely been used due to a lack of knowledge of the effects of fire on these ecosystems. In addition, research in this area is limited and insufficient (Pérez, 2012) and investigations of fire effects on fungal communities have been limited. Although a considerable body of research has emphasized the effects of fire on the status of crop trees (Matias *et al.,* 2010), studies related to the effects of fire on other groups of organisms,

particularly macrofungal communities, has received little attention. It is crucial to study fungal communities that follow prescribed burning events because they play a key role in the decomposition of OM and nutrient turnover rates, which influence ecosystem stability and recovery following disturbance (Ferris *et al.,* 2000; Lindahl *et al.,* 2007; Van Der Heijden *et al.,* 2008; Pietras *et al.,* 2013). Furthermore, no studies have investigated the relationship between fungal community structures, particularly of mycorrhizal species, and edaphic variables in Cuban forest ecosystems. It is important to understand how mycorrhizal fungal communities respond to prescribed burning as they play a vital role in the restoration of the ecosystem after a disturbance (Mediavilla *et al.,* 2014). After the fire, the stress conditions affecting the vegetation can be mitigated by ECM fungi because these fungi can facilitate the acquisition of the required resources for their host plant. Fungal symbiosis is also crucial for post-fire regeneration and survival of *Pinus* spp. seedlings (Buscardo *et al.,* 2009). In addition, soil restoration processes, such as nutrient cycles and organic matter decomposition, are promoted by the action of saprotrophs (Hernández-Rodríguez *et al.,* 2015), which are stimulated just after a fire (Hernández-Rodríguez *et al.,* 2013). Therefore, it is important to know the extent of the fire impact after prescribed burning treatment and what conditions may enhance post-fire growth of the fungal community may be of vital importance for its recovery. Furthermore, studies that have evaluated post-fire fungal succession in different ecosystems have reported that the re-colonization process takes 3 to 5 years in Mediterranean areas (Hernández-Rodríguez *et al.,* 2013) and 5 to 10 years in tropical forests (Dejene *et al.,* 2017).

In order to help forest managers to develop processes to prevent the negative effects of high-severity fires in Cuba's tropical forests, we undertook a pioneer study that was designed to provide baseline information about the effects of two types of prescribed burning (forward burning that acts as a heading fire and back burning that acts as a backfire) on ECM fungal communities under natural stands dominated by *Pinus cubensis* Grisebach trees. The main specific objectives were: (i) to analyze the effects of forward and back prescribed burning on ECM fungal abundance over time; (ii) to analyze whether the recovery of ECM communities following forward or back prescribed burning differs; and (iii) to explain fungal community composition changes in terms of some edaphic variables. The disturbance made by the prescribed burning would not be severe enough to alter the environment substantially but would be sufficient to affect the ECM species. The humid environmental conditions of the studied forests might reduce the severity of prescribed burning effects on fungal communities and, hence, communities might recover quickly after prescribed burning. However, the lower flame heights and lower intensity of backfire burns might enable backfires to move through the stand at a slower speed than forward burning fires (Brown & Davis, 1973). Consequently, the backfire might remain in the soil, enabling raised temperatures to rêach deeper into the soil layer. Thus, we hypothesized that: (1) back and forward burning would have different impacts on fungal sporocarp abundance, with quicker recovery times following forward fire burning than back burning; and (2) changes in fungal composition would be correlated with the type of fire, the time since prescribed burning, and with some edaphic properties, as these variables together with the vegetation characteristics are known to affect fungal succession after a fire (Hernández-Rodríguez *et al.,* 2013).

Material and methods

Study area

The study area is situated in a natural forest (20º 21'51.7" N; -74º 58' 32.3" W) in Yateras, in the most eastern part of Cuba, about 964 km from La Habana, the capital city of the country (Fig. 1). The altitudinal range is between 600 and 1600 m above sea level. The study area is characterized by a tropical climate with a mean annual temperature of 22.9 ºC and annual average rainfall of 2010 mm, most of which falls between May and October. The topography is undulating with slopes ranging from 5 to 7% and the predominant soil is red Ferrallitic (Hernández *et al.,* 1999) over strongly saturated limestone. The forest in the study area is dominated by *P. cubensis* and provides a variety of important ecosystem services such as watershed protection and carbon sequestration. The main secondary species are *Calophyllum utile* Bisse, *Geoffroea inermes* Sw., *Terminalia orientalis* Monachino, *Terminalia nipensis* Alain, and *Coccothrinax orientalis* (León) O. Muñiz & Borhidi.

Prescribed burning treatment

Prescribed burning was carried out in the study area at the beginning of June 2015. A completely randomized design was established to assess the effect of prescribed burning that acts as a heading fire (PBH) and prescribed burning that acts as a backfire (PBB) on the diversity of ECM mushroom taxa and soil characteristics. Heading fire was conducted with slope or downwind; this type of fire typically has a rapid advancement of the front and a shorter residence time of the fire in the soil which may prevent overheating, excessive consumption of organic matter, and high temperature (Vega, 2001). Whereas, backfire was applied with the slope or headwind, with a slow rate of spread, with a shorter flame length and lower fire intensity than heading fire (Vega, 2001). The treatments were carried out in six 20 × 50 m plots: the PBH treatment was performed in plots 1, 2, and 3 (n=3), and the PBB treatment was performed in plots 4, 5, and 6 (n=3). To analyze

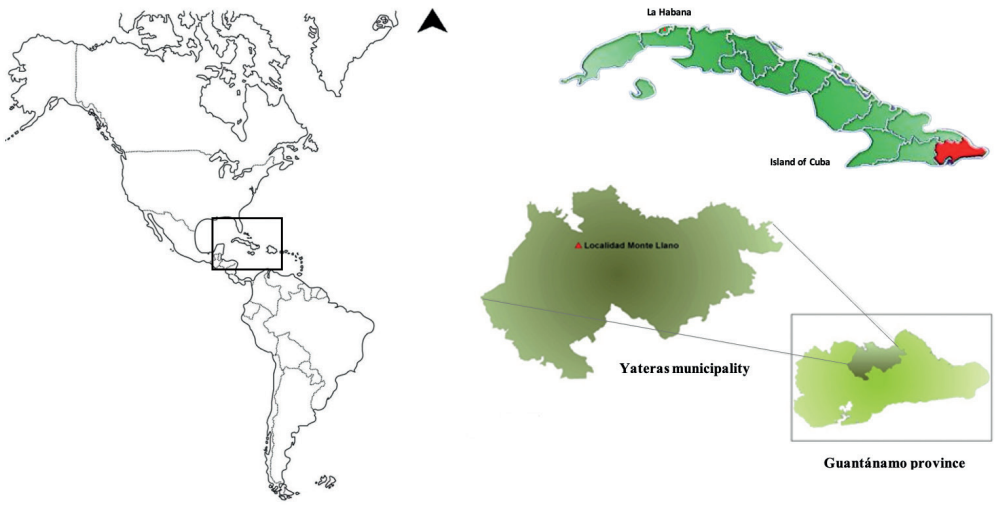

Figure 1. Map of Yateras municipality in Guantánamo province on the Island of Cuba showing the location of the study plots in Monte Llano (America 1:15,000,000).

the effect of these treatments, avoiding the site effect, we also took data before burning in all the studied plots. The characteristics of the PBH and PBB treatments and the fuel load in each plot are shown in Table 1. The rate of spread (*r,* m min^{-1}) was calculated as the mean of several measurements of the time taken for the fire front to travel between two locations of known separation according to Ramos (2010). Based on Bottelho & Cabral (1990) classification system, the *r* during PBH was 'slow' (1.38 ± 0.91 m min^{-1}) and, as expected for a backfire, the *r* during PBB was even slower (0.53 ± 0.06 m min^{-1}). Flame length (*L,* m) was calculated according to Batista (1990); fire-line intensity (*I,* kcal m^{-1} s^{-1}) was calculated using Byram's equation (Byram, 1959).

Table 1. Summary of the characteristics of the two prescribed burning treatments and the fuel load in each of the studied plots.

Type	Variables	PBH		PBB	
		Before	After	Before	After
Fuel	Live biomass (t ha^{-1})	1.538[a]	0.000[b]	0.168[a]	0.000[b]
	Litter (miscellaneous fraction) (t ha^{-1})	22.771[a]	12.740[b]	21.970[a]	9.107[b]
	Dead fuel Class I (1-hour fuels) (t ha^{-1})	2.187[a]	1.707[b]	2.370[a]	1.230[b]
	Dead fuel Class (10-hour fuels) (t ha^{-1})	1.738[a]	1.440[b]	1.947[a]	1.273[b]
	Total (t ha^{-1})	28.235[a]	15.886[b]	27.936[a]	11.611[b]
Soil	pH H2O 1:2.5	5.172[a]	5.465[b]	5.173[a]	5.464[b]
	Organic matter (%)	3.323[a]	4.093[b]	3.325[a]	4.093[b]
	Ca (cmol(+)/kg)	0.813[a]	0.938[b]	0.840[a]	0.941[b]
	Na (cmol(+)/kg)	0.060[a]	0.157[b]	0.050[a]	0.152[b]
	Mg (cmol(+)/kg)	0.320[a]	0.362[b]	0.328[a]	0.366[b]
	P (ppm)	1.113[a]	1.137[a]	1.120[a]	1.139[a]
	K (cmol(+)/kg)	0.140[a]	0.172[a]	0.169[a]	0.168[a]
Fire	Rate of spread (r, m min^{-1}) (Ramos, 2010)	1.38 ± 0.91		0.53 ± 0.06	
	Flame length (L, m) (Batista, 1990)	1.38 ± 0.13		1.10 ± 0.03	
	Fire-line intensity (I, kcal m^{-1} s^{-1}) (Byram, 1959)	145.04 ± 15.82		138.77 ± 10.22	
	The heat released per unit area (H_a, kcal m^{-2})	15,833 ± 100		14,467 ± 986	

Dead fuel Classes III and IV were not found. Different letters indicate significant differences between values ($p<0.05$) based on Tukey Post Hoc Test. Comparisons were made for pair-wise combinations of treatment (before and after prescribed burning treatments) for columns. PBH, prescribed burning that acts as a heading fire; PBB, prescribed burning that acts as a backfire.

Sampling data

Fuel load sampling

To determine the pre-and post-fire biomass in the plots, all the vegetation in four subplots (1 m^2 each) within each 20 × 50 m plot (n=24) was removed a week before and a week after the application of the prescribed burning treatment. Fuel samples comprised live biomass, litter (miscellaneous fraction), and dead fuel. Dead fuel was categorized using the USDA Forest Service fuel classification system (Brown & See, 1981), which is based on time-lag and diameter: 1-hour fuels (<0.6 cm in diameter), 10-hour fuels (0.6 cm to <2.5 cm in diameter), 100-hour fuels (>2.5 cm and <7.5 cm in diameter) and 1000 hour fuels (>7.5 cm in diameter). The biomass was then transported to a laboratory at the University of Guantánamo, where it was oven-dried at 75 °C for a minimum of 48 h until a constant weight was obtained (Prichard *et al.,* 2017). Fuel load was categorized based on biomass weight, as described in previous studies performed in similar ecosystems (Julio, 1996): low (0–20 t ha^{-1}), half (20–40 t ha^{-1}), high (40–80 t ha^{-1}) and very high (>80 t ha^{-1}).

Sporocarp sampling

To understand the effect of prescribed burning on fungal communities over time, nine interval samplings were carried out. A pre-burn sampling a week before the burn was followed by samplings at 15, 30, 45, 60, 75, 90, 105, and 120 days after burning. All individual ECM species found in the plots at the nine sampling times were collected (Martín-Pinto *et al.,* 2006). Most of the species were identified in the field; the rest of the species being identified in the laboratory. In the laboratory, the morphological features of the fruit bodies were examined using appropriate monographs, including for example Heinemann (1956); Singer (1965); Hjortstam & Ryvarden (1996); and Antonin (2007), to determine the fungal species. Taxa and authors' names follow Mycobank (http://mycobank.org).

Soil analyses

To analyze the effect of the prescribed burning treatment on soil variables and relate them to fungal taxa composition, soil samples were taken from each study plot a week before burning and 15, 30, 45, 60, 75, 90, 105, and 120 days after burning. Soil samples were collected from six random sampling points in each 20 × 50 m plots. Plant matter and debris were cleared from the surface before extracting soil to a depth of 20 cm with the aid of an auger and a spade (Guidot *et al.,* 2002; Mediavilla *et al.,* 2020; Vázquez-Veloso *et al.,* 2022). The samples were mixed thoroughly to obtain a composite soil sample for each plot, of which 500 g were transported to the laboratory in a plastic bag before analysis. After air-drying the soil in the shade, the magnesium (Mg^{2+}), calcium (Ca^{2+}), OM, nitrogen (Na^{+}), phosphorus (P_2O_5), potassium (K^{+}) content, and the pH were determined using Complexometric, Tiurin, Oniani, photometry flame or potentiometric methods. The soil analyses were performed by the Official Provincial Laboratory of Soil in Guantánamo belonging to the Cuban Ministry of Agriculture.

Statistical analyses

Differences in variables among treatments such as the number of sporocarps, fuel load, soil variables, and fire variables were assessed using linear mixed-effects (LME) models (Pinheiro *et al.,* 2016). For each model, the analyzed variable was considered as the fixed factor and the plot was selected as the random factor. Linear mixed-effects models were used to prevent false-positive associations due to the relatedness structure in the sampling. A Tukey test was used as a post-hoc test to analyze significant differences ($p \leq 0.05$) among treatments when needed.

The relationship between fungal composition and edaphic parameters was analyzed using non-metric multidimensional scaling (NMDS), based on a Hellinger-transformed species matrix and edaphic scaled data. The effects of time after prescribed burning were analyzed using a Permutational Multivariate ANOVA (PerMANOVA) based on 999 permutations using the ADONIS function in the vegan package. A one-way crossed analysis of similarities (ANOSIMs) was also performed to assess the significance of differences among groups observed in NMDS plots. Isolines of OM were also plotted on NMDS ordinations using the ordisurf function. The strength of the difference between treatments was measured by R values generated by ANOSIM, which take a value from 0 to 1, with 1 being the greatest dissimilarity between treatments (Clarke *et al.,* 2014). Permutation tests using 999 replicates established the statistical significance *(p)* of R values. An analysis of similarity percentages (SIMPER; Clarke, 1993) was also performed to identify the ECM species that were most responsible for the observed patterns and to determine the percentage contributions of these species to significant dissimilarities between the treatments (Parravicini *et al.,* 2010). The analysis was conducted using PAST software (Hammer *et al.,* 2001). Effects of edaphic variables on ECM composition were determined based on the Bray–Curtis dissimilarity matrix. The correlation of NMDS axes scores with explanatory variables was assessed using the *envfit* function in R. To assess the influence of time after prescribed burning, soil fertility parameters, and fire variables on the ECM composition, we used

the Mantel Test using Bray–Curtis distance on the total species matrix.

Results

Changes in sporocarp abundance

Overall, eight ECM taxa were collected from the study plots: *Boletus* sp., *Suillus brevipes* (Peck) Kuntze, *Suillus decipiens* (Berk. & M.A. Curtis) Kuntze, *Suillus* sp., *Amanita muscaria* subsp. *americana* (Lange) Singer, *Lactarius semisanguifluus* R. Heim and Leclair, *Scleroderma stellatum* Berk., and *Pisolithus arhizus* (Scop.) Rauschert. Although prescribed burning had a significant immediate effect on the number of ECM sporocarps found in the study area ($p<0.05$; Fig. 2), the number of sporocarps found in forward and backward burning plots did not differ significantly ($p>0.05$). Significantly fewer sporocarps were collected 15 days after the prescribed fire compared to the later sampling times (Fig. 2; $p<0.05$). Sporocarp production showed an increasing trend with time after the fire treatment in both PBH and PBB plots (Fig. 2), with the greatest number of sporocarps found at the final sampling, 120 days after prescribed burning. However, the number of ECM sporocarps found after 75 and 60 days in the forward and backward burning plots, respectively, did not differ significantly from the numbers found in the plots before the burn ($p>0.05$), indicating that ECM mushroom taxa recovered rapidly after prescribed fire in these forests (Fig. 2).

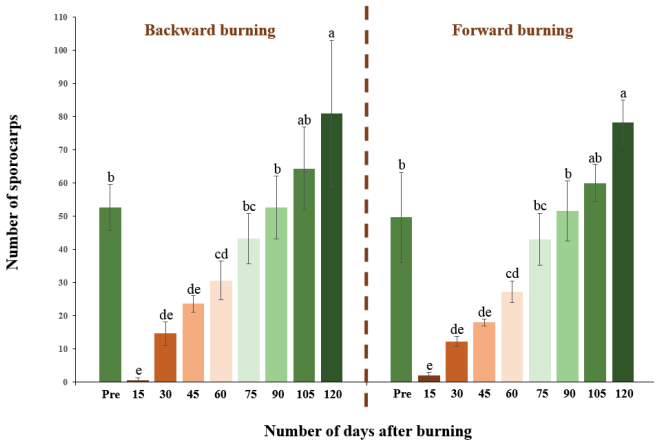

Figure 2. The total number of sporocarps collected 7 days before prescribed burning (Pre) and at 15-day intervals after prescribed burning. The data shown are means ± standard deviation. Different lowercase letters above bars indicate a significant difference ($p<0.05$) in the total number of sporocarps collected at different sampling times for each prescribed burning treatment.

ECM fungal composition and explanatory variables

NMDS based on Bray–Curtis distance followed by perMANOVA analyses confirmed that the fungal composition differed among time categories after prescribed burning (time categories: Pre-burning, 15, 30–45, 60–75, 90–120 days after burning) ($F=14.5$, $R^2=0.54$, $p=0.001$). The ordination showed that the sampling period 15 days after burning was distinct from the other four sampling periods (Fig. 3). This was also confirmed by ANOSIM pair-wise comparisons measuring the strength of fungal composition differences between the five sampling time treatments (Table 2). The SIMPER analysis identified ECM mushroom taxa that typified and distinguished between the collection times after prescribed burning. The cumulative contribution of the most influential species at a 50% cut-off and the cumulative total contribution is shown in Table S1 [suppl]. However, NMDS followed by

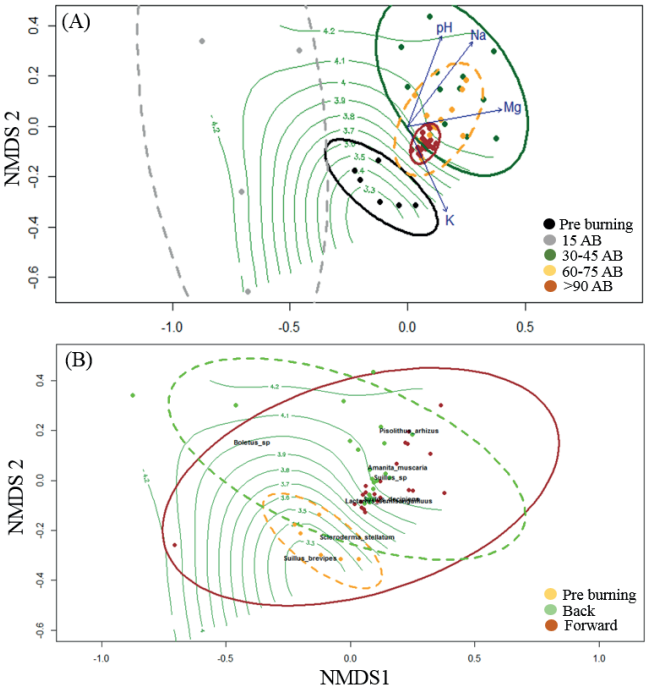

Figure 3. Non-metric multidimensional scaling (NMDS) ordination graph with fitted soil variables (A) and the three burn treatments (B) based on dissimilarities calculated using the Bray–Curtis index of ectomycorrhizal (ECM) taxa community composition with organic matter displayed as isolines. Blue arrows represent environmental variables that were most significantly ($p\leq0.005$) related to ordination. Ellipses in (A) indicate ECM taxa communities in preburned *Pinus cubensis* forest (control) and at 15, 30–45, 60–75, and >90 days after prescribed burning. Ellipses in (B) indicate unburned *P. cubensis* forest (control), prescribed burning that acts as a backfire (back), and prescribed burning that acts as a heading fire (forward). K, potassium; Mg, magnesium; Na, sodium.

Table 2. Overall average dissimilarity and ANOSIM pair-wise comparisons of ectomycorrhizal sporocarp samplings at different time intervals after prescribed burning based on Bray–Curtis distance measures (Global R-value=0.59; p=0.0001).

Pair-wise comparison of collection times	Dissimilarity (in %)	*p*
Pre-burning and 15 days after burn	77.9	0.003
Pre-burning and 30–45 days after burn	42.1	0.000
Pre-burning and 60–75 days after burn	30.7	0.000
Pre-burning and>90 days after burn	23.5	0.000
15 days and 30–45 days after burn	87.4	0.000
15 days and 60–75 days after burn	85.7	0.000
15 days and>90 days after burn	84.4	0.000
30–45 days and 60–75 days after burn	23.9	0.020
30–45 days and>90 days after burn	26.9	0.000
60–75 days and>90 days after burn	14.6	0.001

perMANOVA showed no significant differences in ECM taxa composition between the two prescribed burning treatments (F=1.025; p=0.381).

Variables grouped under edaphic, fire, and time were significantly correlated with ECM taxa composition (p<0.050; Fig. 3; Table 3). According to the Mantel test, the time intervals after prescribed burning contributed the most (64%, p=0.000) to the variation in ECM taxa composition, followed by soil fertility parameters (26%, p=0.002; Table 3) and fire variables (1.13%, p=0.380), though they are not significant. Among the significant soil parameters, OM and Na strongly influenced fungal community structures (Table 3).

Discussion

This study was conducted based on the sporocarps samplings in Caribbean Forest systems in Cuba. Although there is a limitation regarding the control plots, the sporocarps production was sampled weekly in nine sets of permanent plots (20 × 50 m each) from the *P. cubensis* natural forests for about four months. The patterns of sporocarps along the time sequence following fire provided important clues related to the prescribed burning effect on the structure of ECM fungal communities in the studied forest systems. To date, there has been little investigation of the effects of fire on fungal communities in Caribbean forest systems. In this pioneer study, we have explored the impact of prescribed burning on ECM fungal species in *P. cubensis* forests. Although we had expected that the type of prescribed burning treatment would affect the fungal species in the study area, the ECM mushroom taxa community in the heading fire and the backfire plots did not differ significantly. Forest fires typically have short- and long-term effects on fungal species. In the short-term, fire causes a reduction in richness (Kutorga *et al.,* 2012; Reazin *et al.,* 2016); in the long-term, fire also causes a shift in the relative frequencies of fungal species in the forest system (Rincón & Pueyo, 2010; Smith *et al.,* 2017). In

Table 3. Significance of the explanatory edaphic and fire variables for ectomycorrhizal taxa composition based on the Hellinger transformed data matrix. Values in bold indicate highly significant effects (p<0.01). Grouped contribution is shown according to a Mantel test.

Sources	Contribution	Variables	r^2	*p*
Soil fertility	26.42%	pH	0.16	0.019
		Organic matter	0.29	**0.002**
		Na	0.19	**0.007**
		K	0.15	0.023
		Mg	0.17	0.012
Fire variables	1.13%	Intensity	0.002	0.997
		Spread	0.03	0.466
		Heat	0.02	0.666
		Length	0.05	0.260

this study, both burn treatments had an immediate impact on the number of fungal species, with the fewest ECM mushrooms taxa recorded at the first sampling (15 days after burning). This immediate effect could be due to the fire heating the soil, which it is known to reduce active mycelium, especially in the upper soil layers (Cairney & Bastias, 2007), leading to an indirect impact on the growth and maintenance of ECM taxa (Kennedy *et al.,* 2014), particularly of those ECM species that cannot withstand heat or that are unable to survive as fire-resistant propagules (Dove & Hart, 2017). For example, in this study, *Boletus* sp. and *Suillus brevipes* were the only taxa that were observed immediately after prescribed burning. Of these, *Suillus* have been reported in the early-stage succession of Mediterranean fire-affected ecosystems (Hernández-Rodríguez *et al.,* 2013), which suggests that they might have the ability to survive and respond positively to low-severity fires. Furthermore, changes in edaphic variables due to fire could also influence the belowground allocation of plant photosynthates to fungal symbionts. For example, increases in N availability after a fire due to fire-induced mineralization may negatively impact colonization by ECM taxa (Parks *et al.,* 2016; Dove & Hart, 2017). In this study, we observed an immediate increase in the quantity of soil N, P, and Mg in fire-affected plots as compared to the unburned plots. Therefore, the reduction in the number of ECM taxa observed in recently burned areas could be due to soil mineralization. However, the magnitude of the fire effect on fungi probably also depends on the functions that are performed by the different fungal species associated with the vegetation and with other environmental variables. Thus, further explorations of such relationships are fundamental for developing forest management strategies in these fire-affected forest areas.

However, another explanation for the rapid recovery of fungal species in the study plots after prescribed burning could be that the humid environmental conditions reduced the fire severity by influencing the fuel moisture conditions and fuel accumulation. The increasing number of sporocarps observed over time after prescribed burning could support this idea. In PBH and PBB plots, fire-line intensity values ranged from 128.24 to 159.64 kcal m^{-1} s^{-1}. These values agree with those reported by Rodríguez & Molina (2010), who noted that average fire-line intensity values could vary from 101 to 500 kcal m^{-1} s^{-1}. Under these low fire severity conditions, the mycelium of a number of different ECM species in the rhizosphere may be able to withstand the fire effects (Jennings *et al.,* 2012; Hernández-Rodríguez *et al.,* 2015). Thus, 60 days after the PBH and PBB treatments, the number of sporocarps recorded was not significantly different from that prevailing before prescribed burning. The rapid proliferation of sporocarps may also due to the fact that there was a period of intense rainfall in the days following the application of prescribed burning, as June-October represents the months with the higher peaks of precipitation in the year. Claridge *et al.* (2009) reported that after a forest fire, pre-fire fungal communities are largely eradicated, with secondary succession beginning with the first significant rainfall. Four months after the treatment (120 days), sporocarp production was significantly higher than before the treatment, probably due to an increase of some macronutrients after the application of the prescribed burning treatments. Although we could not provide data regarding the weather conditions in the studied plots after burning, this is a relevant environmental factor explaining the response of the ECM fungal community to the perturbation. Despite we could compare the two burning types in similar environmental conditions, this point deserves further investigations. Overall, the two prescribed burning treatments appeared to cause minimal damage in the short-term to ECM taxa (Brown *et al.,* 2013; Oliver *et al.,* 2015) and, thus, the ECM taxa community recovered shortly after the fire.

Although the type of prescribed burning did not significantly affect the ECM fungal community, as expected, the amount of time since the prescribed burning affected the ECM taxa composition. This likely reflects the post-fire inoculum potential of different ECM taxa (Dove & Hart, 2017). The recovery time of different fungal species may differ because soil heating can reduce the amount of active mycelium, especially in the upper soil layers (Cairney & Bastias, 2007). On the one hand, the earlier fruiting patterns observed for some species suggest that these species might have stronger inoculum potential post-fire than others (Baar *et al.,* 1999). On the other hand, the fruiting of the species might also benefit from fire since they form their reproductive structures as a result of fire promotion (Hart *et al.,* 2005). Hence, some level of fire in the ecosystem could provide a higher abundance of fire-loving fungal species, technically called pyrofilous fungi. Differences in fruiting patterns are also likely due in part to phenological differences in the fruiting frequencies of different fungal species, as the fire could also affect soil abiotic conditions such as temperature and moisture (Neary *et al.,* 1999), which are vital for their growth and development but may indirectly affect ECM fruiting (Perry *et al.,* 1989). Similarly, it has previously been demonstrated that ECM taxa are influenced by edaphic variables (Straatsma *et al.,* 2001; Zakaria & Boddy, 2002; Yang *et al.,* 2017). Our small-scale study provides evidence that edaphic variables had a significant effect on ECM taxa distribution. The analysis indicated that soil pH, OM, Na, K, and Mg were correlated with ECM taxa. This might be due to an increase in the quantities of decomposable and burned materials, which could facilitate the production of valuable nutrients through ash deposition (Peay *et al.,* 2010). Fungi typically extend their mycelia at the soil–litter interface (Boddy *et al.,* 2009) and, hence, the significant increase in OM following prescribed burning could influence mycelial outgrowth and network formation

(Zakaria & Boddy, 2002). Organic matter has also been reported to influence ECM taxa communities in other tropical forest systems (Dejene *et al.,* 2017). In addition, OM influences fungi through its impact on the water-holding capacity of soil and the nutrient availability in the soil (Harrington, 2003). Similarly, the influence of K and Mg on fungal species has also been reported (Olchowik *et al.,* 2021), which might be among the factors contributing to an increase in the extent of root colonization and, hence, in the abundance of the ECM taxa. However, given that it is unclear how a particular element influences a particular ECM taxon, further research into this is needed.

Conclusions

The use of an integrated forest management approach in Cuban forests has involved the search for versatile and economic alternatives for fire prevention. This study is the first investigation related to the effect of the immediate impact of prescribed burning techniques on ECM taxa and on their succession in *P. cubensis*-dominated natural forests. This information is vital for managing the collection of valuable fungal species that inhabit these forests, e.g., the edible ones. As expected, both types of prescribed burning showed a significant immediate influence on ECM taxa fruiting. However, ECM taxa communities recovered rapidly in terms of sporocarp fruiting and composition and were unaffected by the type of prescribed burning applied. These findings suggest that the impact of prescribed burning on ECM taxa communities in humid tropical forest systems is low. In these systems, also the humid environmental conditions of the studied forests might have mitigated the severity of prescribed burning effects on fungal communities and, this could explain the quick recovery of the prescribed burning.

Despite the lack of control plots to evaluate the evolution of the fungal communities under untreated conditions, this pioneer study provides a piece of novel information related to the evolution of ECM species following two prescribed burning types, which is important to support the need for fungal conservation in the *P. cubensis*-dominated natural forest systems in Cuba. Also, the baseline information provided in this study could be useful in other regions with similar conditions that are facing forests fires. We also showed correlations between ECM taxa and edaphic variables in *P. cubensis* forest systems. Thus, although further research is needed, we suggest that prescribed burning in humid tropical forest systems can be a myco-friendly forest management tool that could be used to reduce the risk of high-intensity wildfires due to an accumulation of understory fuel in the current context of climate change. However, we should be cautious in prescribed burning practices to ensure the intensity and severity of the fire during the application.

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