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Original article

Wildfire does not affect spore abundance, species richness, and inoculum potential of arbuscular mycorrhizal fungi (Glomeromycota) in ferruginous Canga ecosystems

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ABSTRACT

Canga ecosystems develop over superficial iron crusts with shallow and nutrient-poor soils. Under these conditions, arbuscular mycorrhizal fungi (AMF) play an important role in helping plants to overcome abiotic and biotic stresses. Canga can suffer periodic burning and yet it is unknown what the impacts of fire are to AMF communities. We aimed to compare AMF in Canga areas affected by burning (BC) with those with no previous history of burning (NC). We compared AMF species composition, spore numbers, species richness, and mycorrhizal inoculum potential. The total number of spores, AMF species richness and mycorrhizal colonization measured in the infectivity bioassay were not significantly different between areas. A total of 23 species in 10 genera were recovered, with most species belonging to Gigasporaceae and Acaulosporaceae. BC and NC shared 52 % of AMF species. *Gigaspora albida, Gigaspora gigantea,* and *Dentiscutata heterogama* sporulated exclusively in trap cultures. We concluded that AMF spore communities were not affected by burning in Canga soils as measured by spore abundance, species richness and infectivity. Our data contribute to the inventory of soil biodiversity associated with Canga, a high biodiverse and threatened Brazilian ecosystem.

Keywords: Acaulosporaceae, Canga, Gigasporaceae, Glomeromycota, inoculum potential, mycorrhiza, spore numbers, taxonomic diversity, trap cultures

Introduction

Canga ecosystems are associated with superficial iron crust occurring in Minas Gerais and Pará states in Brazil. These ecosystems are dominated by grasses and sages mixed with shrubs growing on fragmented iron crust and perennial and annual herbs developing in rock crevices. Plant families that dominate in this ecosystem are Poaceae, Asteraceae, Fabaceae, Myrtaceae, and Melastomataceae (Skirycz *et al.* 2014). This ecosystem thrives under severe environmental conditions such as high ultraviolet exposure

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and daily temperatures, strong winds, rapid water loss, and shallow acidic nutritionally-poor soils that can contain toxic levels of aluminum and heavy metals (Jacobi *et al.* 2007; Skirycz *et al.* 2014). Distinct microhabitats can be formed in Canga, mainly due to its occurrence along mountain tops, which contributes to the high alpha and beta diversity of plant communities. For this reason, it is considered an ecosystem with high biodiversity (Skirycz *et al.* 2014). Studies in Canga include the diversity of plant communities (Giulietti *et al.* 2019; Andrino *et al.* 2020), soil fauna (Oliveira *et al.* 2019), and plant growth-promoting bacteria (Felestrino *et al.* 2018; Silva *et al.* 2020). Surveys towards conservation and management purposes were also developed in this ecosystem (Souza-Filho *et al.* 2019; Barbosa *et al.* 2020). Plant communities in Canga resemble savanna vegetation due to the dominance of herbaceous plants, shrubs, and few trees (Skirycz *et al.* 2014). However, information on communities of arbuscular mycorrhizal fungi (AMF) associated with the vegetation occurring in Canga is scarce.

Arbuscular mycorrhizal fungi are soil fungi commonly associated with plants in terrestrial and aquatic ecosystems (Smith & Read 2008). These fungi help plants overcoming abiotic and biotic stress by improving nutrient uptake (especially phosphorus), improving soil aggregation, and decreasing nutrient leaching from the environment (Rillig & Mummey 2006; Gianinazzi *et al.* 2010; Verbruggen *et al.* 2012). Studies of occurrence and distribution of AMF in Brazilian ecosystems associated with different floristic domains revealed a high diversity of these fungi associated with natural vegetation, agroecosystems, and disturbed sites (Stürmer & Siqueira 2008; Maia *et al.* 2020). Natural non-burned plots of Canga have been surveyed for AMF communities by Teixeira *et al.* (2017) and Vieira *et al.* (2018) in the Iron Quadrangle region in Minas Gerais. These authors detected 34 AMF species in 11 genera, with species belonging to Ambisporaceae, Pacisporaceae, Glomeraceae, Acaulosporaceae, and Gigasporaceae. Redundancy analyses showed that AMF communities were associated with organic matter in the dry season and Fe content in the soil in the rainy season, the latter being expected for a Canga soil (Vieira *et al.* 2018).

Richness and structure of AMF communities are affected by biotic factors such as host plant (Eom *et al.* 2000) and by several abiotic factors including fertilization (Lin *et al.* 2012), soil texture (Moebius-Clune *et al.* 2013), temperature and precipitation (Sun *et al.* 2013), and fire (Gibson & Hetrick 1988). Fire may have indirect or direct effects on AMF communities as it impacts plant community composition, soil temperature and water potential (Gibson & Hetrick 1988). In Pakistan, burning decreased mycorrhizal inoculum potential in a scrub type of vegetation but it did not significantly alter AMF spore numbers and community composition (Rashid *et al.* 1997). In North American tallgrass prairies, burning episodes significantly decreased AMF species richness, increased total spore numbers, and affected species abundance differently (Eom *et al.* 1999). For instance, burning decreased the abundance of *Glomus aggregatum* but increased spore numbers of *Claroideoglomus etunicatum* and *G. fecundisporum* (Eom *et al.* 1999). In Mountain Chaco Forests of Argentina, burning affected spore density mainly by influencing species in Acaulosporaceae and Gigasporaceae, but not Glomeraceae (Longo *et al.* 2014). Overall, the effects of fire on AMF communities are hard to generalize, and responses differ in direction and magnitude due possibly to variation in fire characteristics (Longo *et al.* 2014).

Canga ecosystems occurring in the north region of Brazil in the Pará state are surrounded by evergreen tropical Amazonian rainforest in an environment not conducive to natural fires (Schmidt *et al.* 2018). Despite this, Canga vegetation in these regions suffers from occasional natural fires (Neves & Damasceno-Junior 2011). In the Carajas Massif, a fire event was detected in an area of Canga, which set the stage to investigate this research on the effects of fire on mycorrhizal communities associated with ferruginous Canga vegetation. This work aimed to survey and compare species richness and taxonomic diversity of the AMF community occurring in burned and unburned areas of ferruginous Canga. We tested the hypothesis that burning decreases AMF spore number, species richness and mycorrhizal inoculum potential associated with Canga vegetation.

Materials and methods

Study sites and sampling design

The study sites are located in the mineral province of Carajas, state of Pará, Brazil. The climate in the region is tropical, Aw according to Köppen's classification (Alvares *et al.* 2013), with rainy summers and dry winters. Total annual rainfall is 1,827 mm and annual mean temperature is 26.2 °C. Soil samples were collected in October 2015 in two areas of ferruginous Canga: a native area with a recent history of natural burning in 2015 (BC, 06º 19' 52'' S, 49º 58' 32'' W) and a native area with no historic of burning (NC, 06º 23' 47'' S, 50º 22' 31'' W). These two areas were *ca.* 70 Km from each other. Both areas are within the Brazilian floristic domain Amazon Forest, which is part of the world biome Tropical and Subtropical Moist Broadleaf Forests.

In each area, three plots of 5 x 5 m each - adjacent to each other - were delimited during the dry season. From each of these plots, three distinct soil samples, 600-800 g each, were randomly obtained using a 6 cm wide soil corer or a shovel when soil was too shallow, resulting in three samples per plot and nine samples per area. Each sample was composed of three sub-samples obtained with the soil core which amounted for *ca.* 300 g of soil per sample.

Soil samples were placed in plastic bags, and stored at 4 °C until processing.

Soil samples were thoroughly homogenized and an aliquot of 100 cm^3 was used to extract and identify AMF spores and another aliquot of 200 cm^3 was used for soil chemical analyses. A 200 cm^3 subsample was obtained from each sample and pooled, which was used to establish trap cultures and to measure mycorrhizal inoculum potential for each area.

Soil chemical analyses

Soil chemical analyses were performed at the laboratory of Empresa de Pesquisa Agropecuária e Extensão Rural de Santa Catarina (EPAGRI, Chapecó, SC), following the methodology of Tedesco *et al.* (1995). Soil pH was measured in distilled water (1:1, vol/vol). Phosphorus (P) and K^+ were extracted with HCl and H_2SO_4 while 1 M KCl was used to extract Ca^{2+}, Mg^{2+}, and Al^{3+}. Organic matter content was measured by oxidation with a sulfochromic solution and determined using the Walkey-Black method described in Tedesco *et al.* (1995). Data for soil chemical analyses are summarized in Table 1.

Table 1. Chemical soil attributes of burned (BC) and unburned (NC) Canga areas from Pará state, Brazil. Values are means ± standard deviation (n = 9). CEC = Cation Exchange Capacity.

Soil variables	BC	NC
pH	4.38 ± 0.25	4.14 ± 0.23
P (mg/dm^3)	5.09 ± 0.59	3,65 ± 0.43
K^+ (mg/dm^3)	93.33 ± 38.26	146.50 ± 33.46
Al^{3+} (cmolc/dm^3)	1.94 ± 0.43	1.54 ± 0.39
Ca^{2+} (cmolc/dm^3)	1.23 ± 0.34	1.43 ± 0.42
Mg^{2+} (cmolc/dm^3)	0.37 ± 0.11	0.56 ± 0.21
CEC (cmolc/dm^3)	14.16 ± 6.73	24.66 ± 6.88
Organic matter (%)	4.64 ± 0.46	6.14 ± 0.48

AMF spore extraction and identification

AMF spores were extracted from soil using wet sieving (Gerdemann & Nicolson 1963), followed by a sucrose gradient (20%/60%) centrifugation (Jenkins 1964). Briefly, 100 cm^3 of soil from each field sample were placed in a 2 L glass beaker, filled with tap water, and stirred using a glass rod. This soil suspension was poured onto nested sieves with 710 µm and 45 µm openings. Materials retained on the 710 µm sieve were removed and placed in a large Petri plate, and inspected under a dissecting microscope (Stemi 2000, Zeiss, Germany) for AMF sporocarps and spores attached to root pieces. Materials retained on the 45 µm sieve were transferred to 50 mL Falcon tubes containing the sucrose gradient and centrifuged at 700 × *g* for 1 minute. The supernatant was then poured over sieves with 300 µm, 180 µm, and 45 µm openings to facilitate spore separation by size, transferred to Petri plates and observed under a dissecting microscope. Spores were pulled out using an extruded glass pipette and separated by morphotype based on size, color, and shape. Spores were mounted on slides with PVLG (polyvinyl-alcohol lactoglycerol) and PVLG + Melzer's reagent mixture (1:1, vol/vol) and identified under a microscope (Axiostar Plus, Zeiss, Germany). Identification was made by observing spore size, color, presence of ornamentation, spore wall structure, and Melzer's reactions and comparing with original species descriptions and those found at web pages of the International Culture Collection of Arbuscular and Vesicular Arbuscular Mycorrhizal Fungi (INVAM - http://invam.caf.wvu.edu, West Virginia University, USA) and Blaszkowski (2012). Classification at the family level adopted in this study follows that proposed by Redecker *et al.* (2013).

The number of AMF species recovered in each area was used to measure species richness. Frequency of occurrence (F) was calculated as the number of samples that a given species was detected relative to the total number of soil samples per area and expressed as a percentage. Species were classified according to their frequency following Zhang *et al.* (2004) as rare (F ≤ 10%), common (10% < F ≤ 30%), most common (30% < F ≤ 50%), and dominant (F > 50%).

Trap cultures

Trap cultures were established according to Stutz & Morton (1996) to induce sporulation of AMF species that were not sporulating in the field at the sampling time. We established trap cultures for each area by mixing 600 g of field soil with 600 g of sterilized quartzite sand and placed in 1.5 kg plastic pots. Each pot received 40-60 seeds of brachiaria grass (*Urochloa decumbens* (Stapf) R.D. Webster) and plants were kept under greenhouse conditions. Plants were watered as needed and each pot received 100 mL of Hoagland's nutrient solution without phosphorus after 60 days and with phosphorus after 120 days. After five months, a subsample of 100 cm^3 was obtained to extract and identify AMF spores as described above. Part of the substrate of the first growth cycle was diluted with a soil:quartzite sand mix (1:1), in 1.5 kg pots and reseeded with brachiaria grass for a second 5-months growth cycle of trapping.

Mycorrhizal inoculum potential

The bioassay method of Moorman & Reeves (1979) was used to estimate the mycorrhizal inoculum potential (MIP) for each area. For this bioassay, an aliquot (600 g) from the composite sample was diluted with a sterilized substrate (soil + quartzite sand, 1:1, vol/vol) and placed in 270 cm^3 plastic cones. Four cones were established per area and seeded with brachiaria grass. Two seedlings were maintained per cone, and roots were sampled after 45 days, washed under tap water, and stained according to Koske & Gemma (1989). The mycorrhizal inoculum potential for each area was measured by the percentage of mycorrhizal colonization assessed by the gridline intersect method of Giovannetti & Mosse (1980).

Data analysis

Prior to statistical analyses, the total number of spores were transformed using log (x+1) and mycorrhizal colonization measured in the MIP bioassay transformed with arcsin square root (√ %). A paired *t*-test was used to compare spore numbers, mycorrhizal colonization and species richness between areas. These procedures were made using the packages *vegan* (Oksanen *et al.* 2017) and *packfor* (Dray *et al*. 2016) with R version 3.1.3 (R Core Team 2016).

Results

A total of 23 AMF species distributed in 10 genera and four families were detected in NC and BC from field-collected spores (Tab. 2). Gigasporaceae and Acaulosporaceae were represented by 11 and 8 species, respectively, and most species of Acaulosporaceae were found in both areas. Most species were classified as common, with their frequency ranging from 11 to 22 %, and no rare species were detected. *Glomus* sp1 and *Acaulospora morrowiae* were dominant species in both areas. Besides these two species, *Acaulospora* sp7 and *Dentiscutata biornata* in NC and *Scutellospora* sp9 and *Bulbospora minima* in BC were classified as dominant (Tab. 2). Twelve out of 23 species were shared between both areas.

Eight species sporulated in the first or second cycle of trap cultures, seven of them belonging to Gigasporaceae and one to Acaulosporaceae (Tab. 3). Species were detected in the first or second cycle of trap cultures only, except for *D. biornata* detected in both cycles. *Gigaspora albida, Gigaspora gigantea,* and *Dentiscutata heterogama* were detected exclusively from trap cultures.

Total number of spores was 2.5 times higher in BC (1,442 ± 1,277) compared to NC (585 ± 302) but this difference was not significantly different ($p > 0.05$) (Fig. 1A). The number of species per sample ranged from 2 to 10 in BC and from 2 to 8 in NC, but the mean species richness was not significantly different between areas (Fig. 1B). Mycorrhizal colonization of *U. decumbens* in the inoculum potential bioassay did not differ significantly between areas and averaged 15.43 ± 6.08 and 12.58 ± 2.12 in BC and NC, respectively (Fig. 1C).

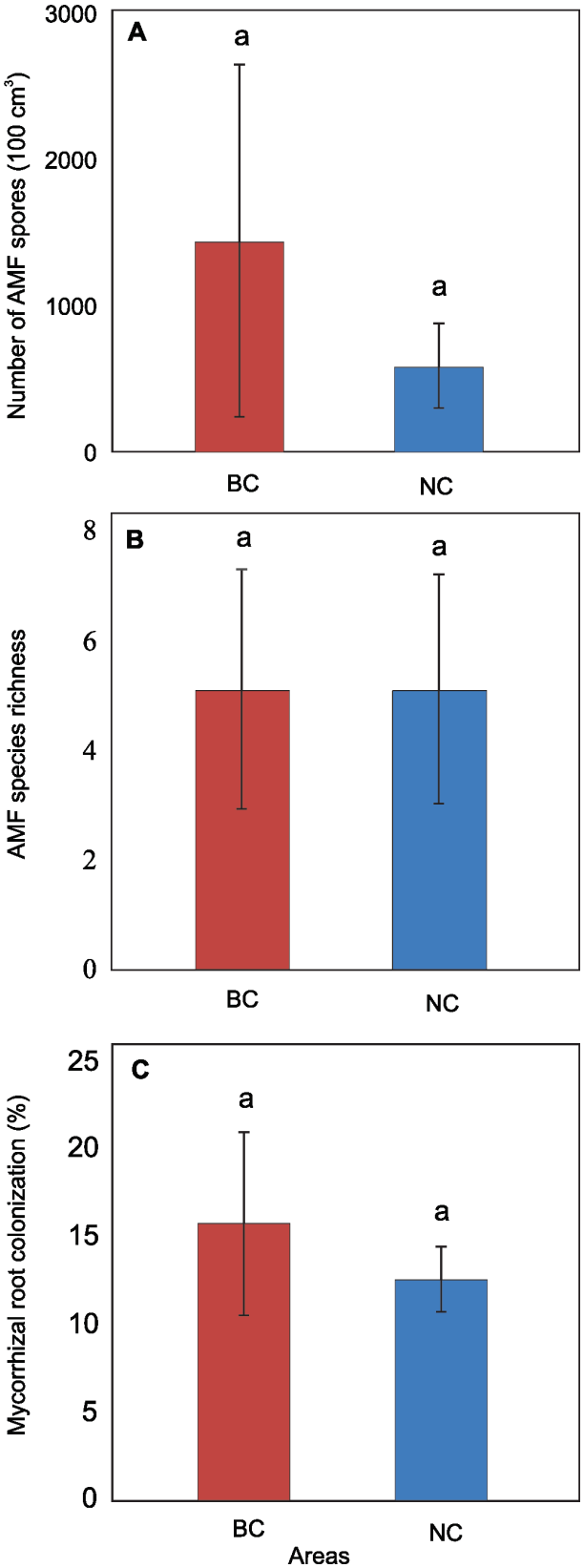

Figure 1. Total number of AMF spores (in 100 cm³ soil) (**A**), AMF species richness (**B**), and mycorrhizal colonization (%) measured in the infectivity bioassay (**C**) from areas of burned (BC) and unburned (NC) Canga. Means (bars) followed by the same letter are not significantly different ($p \leq 0.05$).

Discussion

This study represents the first record of AMF communities associated with ferruginous Canga vegetation in the North region of Brazil, where the Amazon tropical rainforest surrounds this habitat. We used a fire event in a natural Canga area to examine the effect of burning on AMF species richness, spore numbers, and species richness. We recognize that the composition of AMF communities was investigated herein using solely morphological characters from spores recovered from field soils and trap cultures,

with no attempt to use molecular methods. Although a molecular approach using amplicons from the large subunit (LSU) (Delavaux *et al*. 2022) and the small subunit (SSU) (Öpik *et al*. 2010) rRNA genes may be desirable to investigate AMF community composition as complementary to the morphological approach, results published so far have shown that spore morphology can reveal most of the AMF species in a habitat (Wetzel *et al*. 2014; Vieira *et al*. 2018).

AMF communities in Canga were dominated by species of Acaulosporaceae and Gigasporaceae, which together accounted for 78% of the total number of species recovered in NC and BC. Species of both families were also the only sporulators in trap cultures. Studies on soil factors that shape niche differentiation for AMF families indicate that soil pH and soil bulk density are key factors affecting the occurrence of Acaulosporaceae and Gigasporaceae (Lekberg *et al*. 2007; Veresoglou *et al*. 2013). The probability of

Table 2. Frequency of occurrence (F) of arbuscular mycorrhizal fungal species detected in burned (BC) and unburned (NC) Canga from Pará state, Brazil. Species within each area were categorized according to their frequency of occurrence as dominant (D), most common (MC), common (C), and rare (R).

Families	BC		NC	
Species	F (%)	Category	F (%)	Category
Acaulosporaceae				
Acaulospora sp1	33	MC	22	C
Acaulospora foveata Trappe & Janos	-	-	11	C
Acaulospora lacunosa J.B. Morton	11	C	11	C
Acaulospora mellea Spain & N.C. Schenck	33	MC	11	C
Acaulospora morrowiae Spain & N.C. Schenck	78	D	67	D
Acaulospora scrobiculata Trappe	11	C	11	C
Acaulospora sp7	11	C	78	D
Archaeosporaceae				
Archaeospora trappei (R.N. Ames & Linderman) J.B. Morton & D. Redecker	-	-	11	C
Gigasporaceae				
Bulbospora minima Oehl, Marinho, B.T. Goto & G.A. Silva	56	D	-	-
Cetraspora pellucida (Nicol. & Schenck) Oehl, F.A. Souza & Sieverding	11	C	22	C
Dentiscutata biornata (Spain, Sieverding & S. Toro) Sieverd., Souza & Oehl	22	C	56	D
Dentiscutata sp1	22	C	-	-
Gigaspora decipiens I.R. Hall & L.K. Abbott	11	C	-	-
Gigaspora sp1	-	-	11	C
Racocetra fulgida (Koske & C. Walker) Oehl, F.A. Souza & Sieverding	11	C	22	C
Scutellospora sp1	11	C	-	-
Scutellospora sp7	-	-	11	C
Scutellospora sp8	22	C	-	-
Scutellospora sp9	55	D	-	-
Glomeraceae				
Glomus sp1	100	D	100	D
Glomus sp3	-	-	33	MC
Glomus sp4	11	C	11	C
Rhizophagus fasciculatus (Thaxter) C. Walker & A. Schüssler	-	-	22	C

Table 3. Species of arbuscular mycorrhizal fungal species detected in trap cultures (1st and 2nd cycles) established with soils from burned (BC) and unburned (NC) Canga from Pará state, Brazil.

Families	BC		NC	
Species	1st cycle	2nd cycle	1st cycle	2nd cycle
Acaulosporaceae				
Acaulospora morrowiae Spain & N.C. Schenck	-	x	-	-
Gigasporaceae				
Cetraspora pellucida (Nicol. & Schenck) Oehl, F.A. Souza & Sieverding	x	-	x	-
Dentiscutata biornata (Spain, Sieverding & S. Toro) Sieverd., Souza & Oehl	x	x	x	x
Dentiscutata heterogama (T.H. Nicol. & Gerd.) Sieverd., F.A. Souza & Oehl	-	-	x	-
Gigaspora albida N.C. Schenck & G.S. Sm.	-	-	x	-
Gigaspora decipiens I.R. Hall & L.K. Abbott	-	-	-	x
Gigaspora gigantea (T.H. Nicol. & Gerd.) Gerd. & Trappe	-	x	-	-
Racocetra fulgida (Koske & C. Walker) Oehl, F.A. Souza & Sieverding	-	-	x	-

occurrence of Acaulosporaceae increased with high soil acidity and high soil bulk density (Veresoglou *et al.* 2013), while members of Gigasporaceae dominated sandy soils with high bulk density (Lekberg *et al.* 2007). Both factors, acidic soils and high bulk density, are found in Canga soils, explaining the co-dominance of both AMF families found in this study. Soil pH in both areas studied herein ranged from 4.14 to 4.38 (Tab. 1), and it can be as low as 3.76 in Cangas from the Carajá region (Nunes 2009). Soil bulk density is high in Canga compared with adjacent ecosystems, with values ranging from 1.25 to 1.62 g cm^{-3} (Tassinari 2015). Both families were also dominant in Canga habitats in Minas Gerais state, surveyed by Teixeira *et al.* (2017) and Vieira *et al.* (2018). It is interesting that Acaulosporaceae and Gigasporaceae dominated in Canga ecosystems from Minas Gerais and Pará (this study), separated by approximately 1,600 km. Although AMF community assemblages within a similar environment are largely unpredictable based on analyses of virtual taxa (Powell & Bennett 2015), our results suggest that some predictability is possible at the family level for Canga vegetation due possibly to low soil pH and high bulk density. Gigasporaceae and Acaulosporaceae species have traits associated with competition and stress-tolerance, which would be favored in low P environments and in high soil acidity, all respectively (Chagnon *et al.* 2013). These traits could also explain the dominance of members of both families in Canga ecosystems that are depauperate in soil P and have low pH.

At the species level, we also observed some similarities between Cangas from Pará and Minas Gerais. First, most species identified herein were also present in Cangas from Minas Gerais, except *Bulbospora minima, Racocetra fulgida,* and *Rhizophagus fasciculatum*. Second, *Acaulospora morrowiae, A. mellea, A. lacunosa* and *D. biornata* were dominant and common AMF species in Cangas found in Pará (this study) and Minas Gerais (Teixeira *et al.* 2017; Vieira *et al.* 2018). All three *Acaulospora* species have been detected in four or more continents with a cosmopolitan distribution, while *D. biornata* has been detected in three continents (Stürmer *et al.* 2018), which explains their common occurrence in natural ecosystems. A common occurrence of these species suggests that these species are tolerant to the harsh environmental conditions found in Canga ecosystems, turning them into potential species to be used in revegetation programs of Canga. Our study expands the range of occurrence for some AMF species in brazilian floristic domains after the compilation of Maia *et al.* (2020): *Acaulospora lacunosa, Bulbospora minima, Racocetra fulgida, Gigaspora albida,* and *Gigaspora gigantea* are the first report for the Brazilian Amazonian phytogeographic domain, contributing to the biogeography of these species.

We did not find evidence to support our hypothesis that fire would decrease AMF spore numbers, species richness and mycorrhizal inoculum potential in Canga soils. The total number of AMF spores was also not affected by fire in *Araucaria* forest (Moreira *et al.* 2006), in temperate grasslands (Bentivenga & Hetrick 1992; Eom *et al.* 1999), and mountain forests (Longo *et al.* 2014), but burning significantly decreased spore numbers in temperate forest sites (Vilariño & Arines 1991). Fire could be perceived as a stress by AMF which could result in increasing sporulation if fire was severe. Our results suggest that the fire event experienced by the plant community in BC was not severe enough to trigger an increase in spore production by AMF species. Contrasting results are reported on the effect of fire upon mycorrhizal activity, with fire showing no significant effect on mycorrhizal inoculum potential in tallgrass prairie (Bentivenga & Hetrick 1992) but decreased AMF propagule density (Vilariño & Arines 1991). Although burning can raise soil temperature in a depth of up to 3-4 cm (Gibson & Hetrick 1988), this might not be sufficient to affect spores and external mycelium. For instance, Barrett *et al.* (2014) observed that AMF external mycelium length of *Glomus hoi* and *Rhizophagus intraradices* was unaffected by increasing temperatures under experimental conditions. AMF spores are resting structures with relatively thick walls, and this feature might protect them from desiccation or structural changes that impair their viability and survival in soil. We had expected that mycorrhizal inoculum potential would decrease with fire since high temperatures would possibly affect AMF hyphae, which have thinner spore walls compared to spores. Although we did not measure whether hyphal length and activity decreased with burning, it is possible that spore numbers (which were not affected by burning) and colonized root fragments maintained mycorrhizal infectivity in Canga soils after burning. Our results suggest that AMF communities are resilient to a fire event in Canga as the total number of spores and mycorrhizal inoculum potential were of the same magnitude as that found in Canga with no history of burning.

Canga is a very fragile and threatened ecosystem that needs protection and restoration as it is directly affected by open cast iron mining. Taking advantage of a fire event, we demonstrated that AMF communities are not drastically affected by burning occurring in an area compared to areas with no history of burning. This suggests that AMF is an alternative to inoculate plants to be used in revegetation of areas in this ecosystem affected by natural burning. AMF community composition was similar in Cangas from the North region (this study) and those of the Southeast region (Teixeira *et al.* 2017; Vieira *et al.* 2018) of Brazil, which provides some baseline to identify and select AMF species to be used in programs of Canga revegetation and restoration. This study contributes to the biogeography of AMF in Brazilian floristics and the knowledge of soil biodiversity associated with Canga vegetation.

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