



Intense mycorrhizal root colonization in a human-modified landscape of the Caatinga dry forest



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ABSTRACT

Arbuscular mycorrhizal fungi (AMF) symbioses are thought to help plants to cope with harsh environments and to affect not only plant fitness, but also ecological organization from population to ecosystem level. Here, we investigated to what extent this association was present, and what the major environmental drivers were in a human-modified landscape of the Caatinga dry forest in north-eastern Brazil. AMF spore density in the soil and the frequency of AMF root colonization were examined at the species and forest-stand level for the nine most abundant and widespread woody plant species in 18 forest plots across gradients of chronic anthropogenic disturbance, rainfall and soil attributes. Soil spore density was low (1.0 ± 0.6 spore/g soil) across all conditions. However, AMF were present across all species, and colonization frequencies were high (50%, on average) throughout the entire environmental gradients. At species level, AMF colonization frequency only responded to environmental variables (disturbance, rainfall, soil available phosphorus, soil organic matter and soil pH) in one species (*Cnidocolus pubescens*). At forest-stand level, colonization frequency responded positively to both soil pH and rainfall, but not to chronic anthropogenic disturbance. Our results suggest AMF symbiosis is widespread among the plant species and ecological conditions in the Caatinga. Moreover, this symbiosis, which in this case was mediated by rainfall, is likely affecting the resilience of the Caatinga dry forest as it is associated with the most abundant and biomass-relevant forest species and in the harshest conditions for plant survival and reproduction (i.e. nutrient-poor soils and dry habitats).

1. Introduction

Human disturbances are reorganizing the biodiversity of tropical forests, causing impacts from population to ecosystem level, including forest dynamics and ecosystem resilience (Tabarelli et al., 2010; Malhi et al., 2014; García-Valdés et al., 2015). Human-driven disturbances include the continuous removal of small portions of aboveground forest biomass via, for example, firewood collection, exploitation of non-timber forest products and livestock grazing (i.e. chronic anthropogenic disturbance, *sensu* Singh, 1998) by forest-dependent people. This removal of forest biomass can result in more open forest habitats with hotter and drier microclimates (e.g. Hardwick et al., 2015; Marengo and Bernasconi, 2015; Silva et al., 2019), depleted levels of soil nutrients and water content as well as increased compaction (Guadarrama et al., 2014; Schultz et al., 2016; Van der Heyde et al., 2017). Such harsh conditions or high-stress environments have been proposed to reorganise woody plant assemblages (Ribeiro et al., 2019), with cascading effects on biotic interactions (e.g. disruption of mutualisms) and

the ecosystem functions and services they provide (Leal et al., 2014; Oliveira et al., 2019). In addition to chronic anthropogenic disturbances, several tropical biotas are currently experiencing significant impacts due to climate change. At organism level, changes in morphology, phenology and physiology have been observed as a result of climate change (Martínez-García et al., 2012; García-Valdés et al., 2015; Allen et al., 2017). Furthermore, changes in species distribution and abundance (Parmesan and Yohe, 2003; Mair et al., 2014), biotic interactions (Rubenstein, 1992; Martínez-García et al., 2012; Silva et al., 2019) and patterns of ecosystem functioning (Walther et al., 2002; Allen et al., 2017) have been also associated with climate change (Walther et al., 2002). Consequently, there has been increasing concern over the potential connections between local human disturbances and climate change, such as the emergence of physically harsher habitats and their cascading effects on biological organization (Hirota et al., 2011; Rito et al., 2017). For example, reduced rainfall has been a constant threat to seedling recruitment and plant performance across human-disturbed semiarid regions, where soil water availability is

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typically a limiting factor (Brodie et al., 2012; Santos et al., 2014; Allen et al., 2017; Ribeiro et al. 2019).

On the other hand, there is some evidence that symbioses between plants and arbuscular mycorrhizal fungi (AMF) could reduce some of the negative effects of human disturbance and climate change on plant establishment and performance (Violi et al., 2008; Uibopuu et al., 2009). AMF colonize the roots of approximately 80% of terrestrial plants (Smith and Read, 2008). By affecting performance of host plants, e.g. improving seedling survival (Miranda and Miranda, 2001), AMF symbiosis can influence not only plant community structure, but also patterns of ecosystem productivity, nutrient cycling and resilience (Van der Heijden et al., 2015). Indeed, AMF symbiosis may be crucial for plant establishment, especially in the face of soil water deficit, as AMF can increase the gain and transfer of water to the plant through the hyphae (Hardie, 1985; Ruiz-Lozano and Azcón, 1995). AMF symbiosis can also increase soil water retention properties (Augé, 2001; Rillig and Mummey 2006), and improve osmotic adjustment (Augé et al., 1992; Kubikova et al., 2001; Ruiz-Lozano et al., 1995), increase gas exchange and water use efficiency (Augé et al., 1992; Ruiz-Lozano et al., 1995; Frosi et al., 2016b) and protect from oxidative damage generated by drought (Porcel et al., 2004; Porcel et al., 2003; Ruiz-Lozano et al., 2001). Finally, AMF may facilitate the establishment of plants in unfertile soils by increasing their capacity to absorb nutrients, especially phosphorus (Karanika et al., 2008; Dostálek et al. 2013). In synthesis, AMF symbiosis may be crucial for plant establishment because it improves soil aggregation and promotes increased biomass and plant survival in habitats with limiting conditions (Rillig and Mummey 2006; Violi et al., 2008; Frosi et al., 2016b; Pánková et al., 2018).

The Caatinga dry forest covers around 1 million km² in north-eastern Brazil and is the largest and most biodiverse seasonally dry tropical forest (SDTF) globally (Pennington et al., 2009; Silva et al., 2017). Similar to other SDTFs, the Caatinga supports dense rural populations, whose livelihoods are heavily dependent on the use of local natural resources; i.e. forest-dependent people (Silva et al., 2017). Additionally, the Caatinga biota is expected to experience a decline in rainfall of 22% by 2100 (IPCC, 2014). Increased human disturbance, low soil fertility (particularly in sandy soils) and reduced water availability, as well as frequent prolonged droughts as a result of declining rainfall, might favour AMF symbioses due to the harsher conditions imposed by these abiotic factors. Thus, verifying the extent to which AMF colonization is affected by disturbance, climate regime and soil conditions is essential to understand the importance of this association to the establishment of woody plants in the Caatinga dry forest. This is particularly relevant as AMF symbioses are essential for plant establishment and performance.

Here, we examined the relevance of AMF symbioses in a human-modified landscape in the Caatinga dry forest in north-eastern Brazil and their driving forces. More precisely, we assessed soil spore density at forest stand level and AMF root colonization across the nine most abundant woody plant species (i.e. species level) and at forest stand level across our focal landscape. In addition, we investigated the potential impacts of chronic anthropogenic disturbance, rainfall and soil attributes on these symbiosis-related attributes. We expected higher spore densities and frequencies of effective colonization as chronic human disturbance increased and soil fertility and rainfall decreased, because sporulation often increases under such stressful conditions (Zangaro et al., 2013), while AMF colonization would favour plant establishment and growth via better uptake of soil water and nutrients (Augé, 2001; Caravaca et al., 2003; Alguacil et al., 2011; Van der Heyde et al., 2017). Finally, we discuss the uncovered patterns in light of the drivers of these symbioses and their ecological relevance, including for the resilience of the Caatinga dry forest.

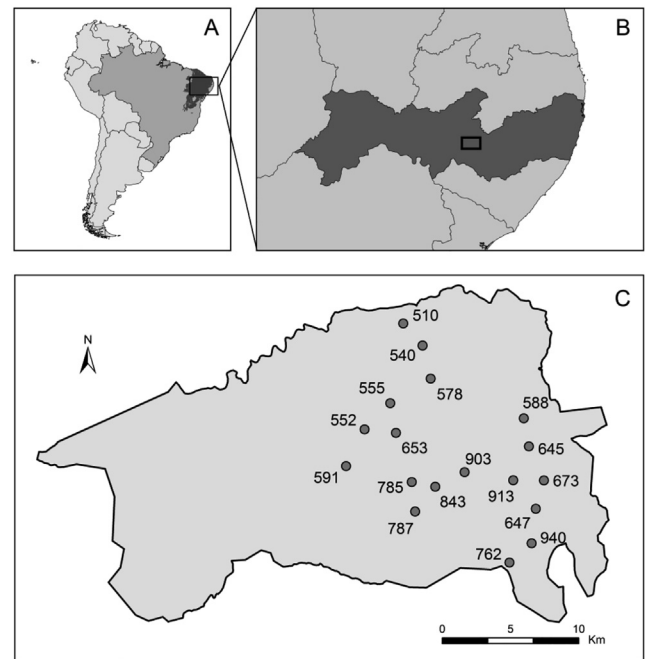


Fig. 1. Study region in north-eastern Brazil (a), and the study landscape (rectangle) in Pernambuco state (shaded area in b). Limits of Catimbau National Park with the 18 study plots represented by dots (c). Numbers in (c) represent the mean annual precipitation in mm for each plot.

2. Material and methods

2.1. Study site

The study was conducted in the Catimbau National Park, a 607-km² protected area in north-eastern Brazil (Fig. 1). The regional climate is semi-arid and is classified as *BSh*, transitioning to rainy tropical (*As'*) in some areas (Köppen system). Mean annual rainfall varies markedly in the Catimbau, from 1100 mm in the south-east to 480 mm in the north-west, with a mean annual temperature of 23 °C (Rito et al., 2017). Approximately 70% of the park landscape is covered by naturally impoverished quartzite sandy soils, supporting low stature (up to 12 m) Caatinga dry forest (Rito et al., 2017). Fabaceae, Euphorbiaceae, Boraginaceae and Burseraceae are the most important woody plant families, while the herbaceous understory is dominated by Cactaceae and Bromeliaceae (Rito et al., 2017).

2.2. Chronic anthropogenic disturbance, rainfall, soil attributes and woody plant assemblages

A long-term ecological research initiative established a network of 18 0.1-ha permanent plots in the Catimbau National Park, distributed along independent gradients of chronic anthropogenic disturbance and rainfall (Rito et al., 2017). All plots were on sandy soil, had similar slope, and supported old-growth vegetation that had not experienced slash-and-burn agriculture for at least 50 years (Rito et al., 2017). Plots were separated by a minimum of 2 km and occurred within an area of 214 km² (Rito et al., 2017).

Briefly, the degree of chronic anthropogenic disturbance was characterized for each plot using a global multi-metric disturbance index, which combined the three main sources of local disturbance: grazing by livestock, wood extraction and exploitation of non-timber products (Arnan et al. 2018). These sources of disturbance were quantified for each plot using socioecological data from surrounding farms and towns, geographic distances from farms and roads, along with direct measurements taken within the plots (Arnan et al., 2018). This multi-metric

disturbance index was standardized to range from 0 (no disturbance) to 100 (maximum possible disturbance), and actual values ranged from 2.7 to 58.1 (Arnan et al., 2018). The mean annual precipitation for each plot was obtained from the WorldClim global climate data repository (Hijmans et al., 2005) with 1 km resolution using the “*maptools*” package (Bivand and Lewin-Koh, 2015) for R 3.1.2 (R Core Team, 2015). Soil attributes were characterized using five samples of the upper 20 cm of soil in each plot, which were pooled into a single soil sample per plot (see Souza et al., 2019). Soil samples were analysed by a private agronomic lab following the Brazilian standard protocols for agronomic analyses (Embrapa, 1997). We used available phosphorous in soil (21.3 to 74.4 mg dm^{-3}), soil pH (4.2 to 6.2) and soil organic matter content (4.4 to 42.4 g kg^{-1}) to estimate soil fertility. Data on relative abundance of species and aboveground biomass were obtained from Rito et al. (2017) and Souza et al. (2019), respectively. We used a principal component analysis (PCA) to investigate whether any of our explanatory variables were correlated. Aboveground biomass and rainfall were found to be correlated, so we excluded aboveground biomass from our analyses.

2.3. Focal plant species

We focused on sampling and analysing soil mycorrhizal spore density and root colonization for the nine most-abundant and widely distributed woody plant species of the Caatinga focal landscape (Table S1 Supplementary material, Rito et al. 2017). We sampled adult individuals (i.e. diameter at soil height > 3 cm and height > 1.0 m, *sensu* Felfili et al., 2005) of our nine focal species that were physically isolated from other plants (minimum radius of 30 cm) to prevent the roots of other individuals from being collected during sampling. We aimed to sample three individuals per species per plot, but the number of individuals per species varied according to the abundance of individuals conforming to our selection criterion. One to three individuals were sampled per species per plot, with a total of 224 individuals sampled throughout our focal landscape (Table S2 Supplementary material).

2.4. Plant-AMF symbiosis

To investigate the relevance of AMF symbioses in the Caatinga dry forest, we examined two variables: soil spore density and percentage of root colonization (i.e. colonization frequency). To assess soil spore density in each of our 18 plots, five 500-g samples of the upper 20 cm of soil were randomly collected in each plot during the wet season. These five samples per plot were pooled into a single sample in sealed bags and transported to the laboratory to quantify the number of spores and sporocarps (adapted from Silva et al. 2014). A subsample of 100 g of each soil sample was wet-sieved (Gerdemann and Nicolson, 1963) before centrifugation (1048g) in water and sucrose (Jenkins, 1964). The number of spores was counted under a stereomicroscope at $40\text{--}100\times$ magnification and converted to number of spores per g of soil.

AMF root colonization frequency at the plant species level was estimated by collecting a minimum of 3 g of roots together with the rhizosphere from the base of the stem of each focal plant. Root harvesting was carried out in the rainy season to allow the identification of deciduous species based on vegetative and/or reproductive characteristics. Collected roots were taken to the laboratory, where fine roots were selected and kept in 50% alcohol. Roots were clarified with 10% (w/v) KOH for 24 h at room temperature, washed with distilled water and stained with trypan blue (w/v) for 1 h (adapted from Koske and Gemma, 1989). Two glass microscope slides per individual were assembled with 25 1-cm root fragments each (totalling 50 cm of root length per individual) for analysis under a microscope with $40\times$ magnification (Giovannetti and Mosse, 1980). Root fragments with any AMF structures (i.e. arbuscles, vesicles or hyphae) were considered to be colonized (Frosi et al., 2016a). Colonization frequency was

calculated as $F = n/N \times 100$, where n is the number of colonized fragments and N is the total number of fragments. This equation was used to calculate colonization frequency per species per plot, as well as colonization frequency per plot by pooling all species in each plot (as adopted Meng et al., 2015).

2.5. Data analysis

We used a general linear model (GLM) to test for the separate and combined effects of our explanatory variables (chronic anthropogenic disturbance index, rainfall and soil available phosphorus, pH and organic matter) on plot-level spore density. To investigate potential effects of our focal species on soil spore density at plot level we used two complementary analyses: (1) a canonical correspondence analysis (CCA) using the relative abundance of the focal plant species per plot and plot level spores density; and (2) a GLM for each focal plant species considering all explanatory variables for the respective subset of plots where each species occurred. For GLMs at species level, the Bonferroni correction was adopted to avoid type I errors, and $p < 0.005$ was adopted as the probability value.

GLMs were also used to investigate the effects of our explanatory variables (chronic anthropogenic disturbance index, rainfall and soil available phosphorus, pH and organic matter) on mycorrhizal colonization frequency at species and plot level. A GLM that included all explanatory variables was used for each species (species level analysis). Again, we used the Bonferroni correction to avoid type I errors and adopted a probability criterion of $p < 0.005$ for species level colonization frequency. To evaluate the variation of colonization frequency within and across species we used a nested ANOVA, in which plant species was considered a nested factor within plot. Colonization frequencies (expressed as percentages) were transformed prior to statistical analysis using the following equation $\sqrt{\arccosine(x)}$ (Frosi et al., 2016a). Data were analysed using R Studio (Version 1.1.463) with the “*lme4*” package (Bates et al., 2019) for GLM and the “*vegan*” package (Oksanen et al., 2019) for CCA.

3. Results

3.1. AMF spore density in the soil

Across plots, soil AMF spore density ranged from 0.31 to 2.03 spores/g (~ 7 fold variation) and averaged 1.0 ± 0.6 spores/g. Spore density at the plot level was not correlated with disturbance, rainfall, or soil available phosphorus, pH or organic matter content (GLM, $p > 0.15$). It was not revealed any significant relationship between the abundance of focal species and spore density by either CCA or GLM analyses.

3.2. AMF root colonization

At species level, AMF mycorrhizal structures, such as spores, hyphae and vesicles, occurred in each of the focal plant species, with a minimum frequency of one colonized plant individual per species per plot and a maximum of all sampled individuals of a given species in all plots (e.g. *Erythroxylum revolutum* and *Trischidium molle*). Species colonization frequency (as calculated based on colonized root fragments) varied greatly within and across species, with a mean colonization frequency per species of $\sim 50\%$ (Table 1). For *Cnidocolus pubescens*, colonization frequency was related to environmental conditions, responding positively to rainfall, and soil available phosphorus and pH, while responding negatively to disturbance and soil organic matter content (GLM, $p < 0.005$, Table 2).

For the remaining eight species, colonization frequency was not correlated with either disturbance, rainfall, or soil phosphorous availability, pH or organic matter content, nor was it correlated with the interactions between these variables (GLM, all $p > 0.005$). A nested

Table 1

Arbuscular mycorrhizal colonization frequency per species for nine focal tree species across 18 plots in the Caatinga dry forest, Brazil. The range indicates the colonization variation within the individuals of each species. The average indicates mean values of root colonization per species (\pm SD).

Species	AMF root colonization range (%)	AMF root colonization average (%)
<i>Cenostigma microphyllum</i> (Mart. ex G. Don) E. Gagnon & G. P. Lewis)	16.7–94.0	46.9 \pm 5.7
<i>Trichidium molle</i> (Benth.) H. E. Ireland	20.0–89.0	59.0 \pm 6.5
<i>Jatropha mutabilis</i> (Pohl) Baill.	3.0–79.9	49.6 \pm 8.3
<i>Cnidocolus pubescens</i> Pohl	29.8–84.0	56.1 \pm 5.5
<i>Colicodrendron yco</i> Mart.	7.6–84.7	55.4 \pm 8.5
<i>Pityrocarpa moniliformis</i> (Benth.) Luckow & R. W. Jobson	9.5–82.7	39.1 \pm 5.5
<i>Commiphora leptophloeos</i> (Mart.) J. B. Gillett	7.1–78.7	58.4 \pm 9.6
<i>Annona leptopetala</i> (R.E.Fr.) H. Rainer	3.4–85.0	45.3 \pm 12.4
<i>Erythroxylum revolutum</i> Mart.	3.2–53.0	37.1 \pm 9.6

ANOVA showed no difference in colonization frequency at species level ($p = 0.07$), but did show a difference at plot level ($p < 0.001$) with no clear pattern related to the direction of response.

Finally, at forest stand or plot level (i.e. pooling all root fragments from the nine focal species in each plot), colonization frequency varied between 8.9 and 86.9% (an almost 10-fold variation) across the 18 plots (Table S3 Supplementary material). Colonization frequency was positively correlated with rainfall and soil pH, with a significant interaction between these two variables (GLM, $p < 0.05$, Table 2). Plants in acid soils (low pH) that receive little rainfall had the lowest colonization frequencies (Fig. 2).

4. Discussion

Our results suggest that soils in human-modified landscapes of the Caatinga dry forest support variable, but relatively low AMF spore densities. In contrast to our expectation, spore density was not affected by chronic anthropogenic disturbance, rainfall or soil attributes. Despite these relatively low spore densities, AMF symbiosis appear to be widespread in such landscapes as all our focal species exhibited some level of root colonization. Disturbance, rainfall and soil attributes appear to have little effect on AMF colonization at species level, as we only observed the effects of these factors on a single species, *Cnidocolus pubescens*. However, AMF colonization at community or forest stand level is positively affected by both rainfall and soil pH, as well as their interaction. In synthesis, AMF symbiosis is a conspicuous interaction in

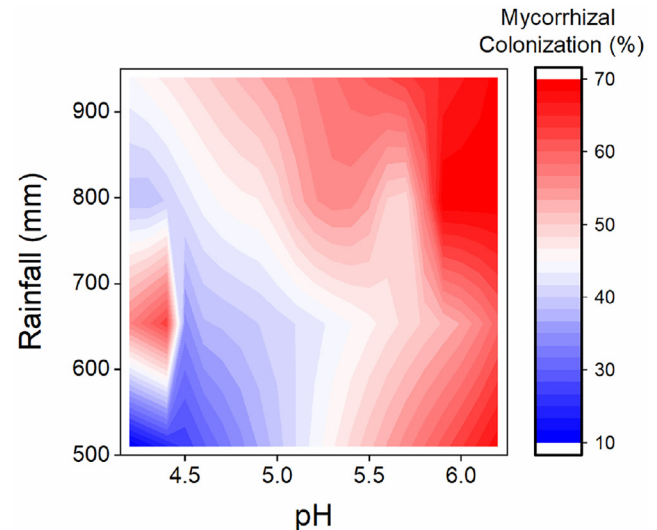


Fig. 2. Contour plot showing model results for the interactive effects of rainfall and soil pH on the mean frequency of arbuscular mycorrhizal colonization for nine focal tree species across 18 plots in the Caatinga dry forest, Brazil.

Table 2

Results of general linear models (GLM) examining the separate and combined influences of chronic anthropogenic disturbances, rainfall, and soil available phosphorus (P), pH and organic matter (OM) on the frequency of arbuscular mycorrhizal colonization in nine focal tree species across 18 plots in the Caatinga dry forest, Brazil. For *Cnidocolus pubescens*, we have presented GLM results for the 11 plots in which it occurred. For each variable, we have indicated the mean coefficient (β), the mean coefficient standard error (SE β), the 95% confidence intervals (95% CI) and the p-value. Significant results ($p < 0.05$ for community level and $p < 0.005$ for species level) are in bold.

Species/Variable	β	SE β	CI - 95%	CI + 95%	p-value
<i>Average Mycorrhizal Colonization</i>					
Disturbance	-0.19	0.21	-0.64	0.26	0.37
Rainfall	0.65	0.21	0.20	1.10	0.01
P	-0.07	0.22	-0.54	0.40	0.75
Organic matter	-0.25	0.22	-0.73	0.24	0.29
pH	0.62	0.20	0.20	1.05	0.01
Rainfall \times pH	0.65	0.19	0.25	1.05	0.00
<i>Cnidocolus pubescens</i>					
Disturbance	-1.07	0.21	-1.62	-0.53	0.002
Rainfall	1.07	0.16	0.67	1.48	0.004
P	0.84	0.16	0.43	1.25	0.001
Organic matter	-0.63	0.13	-0.96	-0.31	0.003
pH	1.05	0.15	0.66	1.45	0.004
Disturbance \times Rainfall \times P \times OM	-1.71	19.57	-56.05	52.63	0.93
Disturbance \times Rainfall \times P \times pH	2.11	0.62	0.40	3.83	0.03
Disturbance \times Rainfall \times P \times OM \times pH	8.99	9.56	-17.54	35.53	0.40
Disturbance \times P \times OM \times pH	-15.63	6.66	-34.10	2.85	0.08
Rainfall \times P \times OM \times pH	4.16	1.54	-0.11	8.44	0.05
Disturbance \times Rainfall \times P \times OM \times pH	2.76	27.15	-72.62	78.14	0.92

human-modified landscapes of the Caatinga dry forest over sandy soils, being mediated by soil attributes and rainfall.

Our findings indicate low AMF spore densities compared to other areas of the Caatinga (e.g. 4–6 spores/g of soil, Mergulhão et al., 2007; Silva et al., 2014), but within the range found by others for this ecosystem (i.e. < 2 spores/g of soil, Silva et al., 2001; Souza et al., 2003). Higher spore densities have been found in the Caatinga dry forest in less acid and clay-based soils (i.e. crystalline basement) (Souza et al., 2003; Mello et al., 2012; Silva et al., 2014), suggesting soil attributes as key drivers of spore persistence and density. Thus, a combination of soils with high sand content (i.e. low water retention) and low pH, in addition to the frequent long-lasting droughts (Yang et al. 2011), apparently reduces spore densities.

Although our landscape supports low spore densities (i.e. low potential for AMF colonization), it was documented high rates of root colonization (i.e. 50% for most species) across a wide range of conditions regarding human disturbance, rainfall and soil attributes. It is well known that across dry forests, such as the Caatinga, AMF species are able to produce more hyphae and increase fungal mycelium in drier areas (Augé, 2001; Ruiz-Lozano, 2003), increasing water and nutrient uptake as well as foliar photosynthesis activity (Zhang et al., 2016). However, it is important to mention that AMF colonization has been proposed to decrease under extremely severe water restriction (Augé, 2001). Apparently, some plant species are not able to maintain intense symbioses through long drought events due to reduced assimilated carbon, i.e. in such severe limiting conditions, the production of photoassimilates becomes low and it is no longer viable for the plant to provide them to the fungi (Barros et al., 2018). Our findings add some evidence for the negative effect of severe water restriction on AMF-plant symbiosis as root colonization was negatively affected by rainfall at the forest stand level. Therefore, it is expected that plants can better afford the metabolic costs imposed by AMF symbioses when under suitable conditions for plant growth (Frosi et al., 2016a), which results in more frequent, intense and diversified associations (Souza et al., 2016).

Finally, constant removal of forest biomass (i.e. chronic anthropogenic disturbance) apparently has no negative impact on plant-AMF symbiosis in the Caatinga dry forest. However, other human-driven disturbances may affect plant-AMF symbiosis. For example, the Caatinga is expected to experience a significant decrease in rainfall associated with anthropogenic climate change (IPCC, 2014). According to our findings, this is not a promising scenario for plant-AMF symbiosis in the Caatinga dry forest, at least in terms of colonization frequency, since plants are unable to maintain symbiosis in the face of extreme drought conditions (Augé, 2001; Frosi et al., 2016a). This scenario is even more concerning when considering that AMF encompasses an immense number of fungus species (Van der Heijden et al., 1998; Silva et al., 2014; Marinho et al., 2019), which collectively cover a wide range of both natural and disturbed habitats, including acid/im-poverished soils (Van der Heyde et al., 2017; Guadarrama et al., 2014), as documented here. It supports AMF symbiosis as a mechanism of ecosystem resilience under threat from chronic anthropogenic disturbance and climate change.

In this ecological context, it is worth mentioning that *Pityrocarpa moniliformis*, which exhibited a colonization frequency of 39%, has been considered a proliferating, disturbance-adapted tree species, accounting for 15% of forest aboveground biomass in our focal landscape (Rito et al., 2017; Souza et al., 2019). This key ecological role can be extended to other focal species (e.g. *Cenostigma microphyllum*, *Jatropha mutabilis*, *Cnidocolus pubescens*, and *Trischidium mole*), as collectively, they represent a substantial portion of forest biomass and stem abundance (see Table S1, Rito et al., 2017; Souza et al., 2019). As the Caatinga dry forest is an ancient biota (late Miocene) with many lineages that spread through other dry forest biotas across the American continent (Queiroz et al., 2017), it seems reasonable to assume that plant-AMF symbiosis has a long evolutionary history, allowing this dry

forest to cope with very harsh conditions such as impoverished, desiccated, acid soils and frequent droughts. This suggests plant-AMF symbioses will play an important role in the current scenario of changes in land use and regional climate in the Caatinga dry forest, with unknown impacts on forest resilience (Brodie et al., 2012; Martínez-García et al., 2012).

In synthesis, plant-AMF symbiosis seems to be an important element of the Caatinga dry forest as it is present across the most abundant and widely distributed woody plant species and in a wide range of ecological conditions in terms of chronic anthropogenic disturbance, rainfall and soil attributes. Despite the occurrence of sites supporting low soil spore densities, species and stand level colonization frequency can be considered high, showing the efficiency of spores in establishing symbioses with plants. Moreover, plant-AMF symbiosis responds to some soil attributes (particularly pH), rainfall and the presence of particular plants, with more alkaline and humid habitats supporting higher levels of plant colonization. Such a close relationship probably represents a key asset for Caatinga resilience in a context of land use and climate change, and as such deserves further investigation.

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.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.117970>.

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