

RESEARCH ARTICLE

Arbuscular mycorrhizal fungi communities shaped by host-plant affect the outcome of plant–soil feedback in dryland restoration

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Abstract

1. Plant inoculation with arbuscular mycorrhizal fungi (AMF) can be a useful tool to overcome challenges in dry forest restoration. However, advances are still needed to guide choices regarding soil origin and inoculum production methods, since outcomes can vary due to plant–soil feedbacks (PSF). We evaluate how soil origin and host plant used for inoculum production affect AMF community and therefore the plant biomass accumulation and functional traits.
2. In the conditioning phase, we investigated whether soils originating from a recovered area (Quarry) and a vegetation fragment (Caatinga) would have their AMF communities modified due to the growth of *Sorghum bicolor* (used for inoculum production) and *Senna uniflora* (used in Brazilian semiarid restoration). In the feedback phase, we compared the performance of four plants species growing on a degraded soil and inoculated or not by a mixture of AMF isolates in comparison to soil inoculum prepared from the conditioning phase.
3. The inoculum from Caatinga presented seven times more AMF species compared to that from the Quarry, which presented ruderal and stress tolerant species. The soil inoculum conditioned by *S. uniflora*, regardless of origin, presented greater evenness compared to the soil inoculum produced with *S. bicolor* and promoted 33% more plant biomass compared to the control without inoculation. Root colonization by AMF increased PSF and decreased plant investment in functional traits such as specific root length (SRL) and specific leaf area (SLA).
4. Our results demonstrate the importance of adopting strategies that preserve local adaptation of inoculants produced. The use of native plant for propagation of native AMF in the conditioning phase provided more positive responses for *Mesosphaerum suaveolens* and *Rhizophodon echinus* than inoculated with introduced AMF isolates. This is probably due to the interaction of inoculated plants with responsive AMF present in the soil.

5. *Synthesis and applications.* Our study shows that conditioning field-collected soil with *Senna uniflora* and using it for inoculation can be a simple technique to promote biomass accumulation for other native herbaceous species. This preserves the compatibility between the soil inoculum produced with native AMF and native plants, representing an important tool for restoration programs.

KEYWORDS

arbuscular mycorrhiza, desertification, inoculum origin, native mycorrhizae, recovery of degraded areas, restoration ecology, soil conditioning

1 | INTRODUCTION

Plant–soil feedback (PSF) refers to the performance of plants after alterations in soil conditions (biotic and abiotic) caused by the same or another plant species (Bennett & Klironomos, 2019; Bever et al., 2010). These responses can be positive when plant performance increases, or negative when it decreases (Bever et al., 1997). Previous studies have shown that increased interaction with soil microorganisms, particularly arbuscular mycorrhizal fungi (AMF), leads to higher biomass production in plants (positive PSF) (Cortois et al., 2016; Semchenko et al., 2018). On the one hand, plant identity strongly affects AMF in PSF experiments (Semchenko et al., 2018). On the other hand, AMF community composition is influenced by plant investment in root functional traits (Eissenstat et al., 2015; Francioli et al., 2021; Sweeney et al., 2021) and, by weak or non-existent relationships with leaf functional traits (Semchenko et al., 2018; Sweeney et al., 2021). Plants may also show higher percentages of root colonization in roots with shorter specific root length (SRL) (Cortois et al., 2016; Semchenko et al., 2018; Zhang et al., 2019). This may occur for morphological reasons, as plants with lower SRL tend to have larger root diameter and more root cortex area available for interaction with AMF (McCormack & Iversen, 2019; Reinhardt & Miller, 1990). This suggests that interventions adopted to intensify AMF-plant interaction should be considered strategically, aiming to optimize PSF results.

Deeper understanding of PSF mechanisms mediated by native mycorrhizal fungi has yielded promising results for ecological restoration (Kozioł et al., 2021). A common goal in ecological restoration projects is to advance the successional status of a given community by increasing the biomass and survival of late-successional plants. In this regard, different studies have shown that late successional plants exhibit positive feedbacks, while ruderal plants present negative feedbacks (Kardol et al., 2006; Kozioł & Bever, 2019). However, early successional plants are important for initiating the ecological restoration process of degraded areas, because in a post-disturbance condition late successional plants tend to be observed less frequently (Swanson et al., 2011). Wubs et al. (2019) have also demonstrated negative PSF in early successional plants when they received soil from remnant vegetation, however, positive PSF was achieved when using inoculated soil from long-term agricultural activity. This highlights that the origin

of the soil inoculum can drive the feedback outcome in early successional plants as well.

The functionality of mycorrhizal interaction also depends on the structure of the community associated with plant roots. It has been evidenced that inoculants with a higher richness of AMF species increase the accumulation of plant biomass (Hoeksema et al., 2010). However, similar growth patterns can be achieved when inoculating an efficient plant growth promoter isolated or mixed with others species (Bennett & Bever, 2007; Crossay et al., 2019). These finds reinforce that the effects of AMF on plants can be associated with an individual species, despite great variation in studies (Powell & Rillig, 2018). In this sense, it is reasonable to suggest that some species might be key for functioning of the total community (Rodríguez & Durán, 2020). Corroborating these finds, Kozioł and Bever (2019) suggested that composition of AMF species might be more important to provide benefits to the host than richness. They showed that AMF species evenness affect plant diversity. However, few studies have emphasized the influence of the AMF community evenness on primary production.

Plant inoculation is one of the strategies proposed for the UN Decade on Ecosystem Restoration (Aronson et al., 2020). Projects in semi-arid ecosystems that have adopted this strategy have recorded higher plant survival compared to the application of hydrogel, organic matter, and tree shelter (Piñeiro et al., 2013). Restoration success can be enhanced by inoculating plants with soil originating from reference ecosystems (Neuenkamp et al., 2019), and thus the origin of soil inoculum can determine the trajectory of plant species composition and microorganisms in areas under processes of restoration (Wubs et al., 2016). However, as a practical matter, commercial inoculants may be preferred, resulting in unsatisfactory plant performance in the field (Maltz & Treseder, 2015). Isolates of AMF from culture collections as well as commercial inoculants are produced with plants such as *Zea mays*, *Sorghum bicolor*, and *Paspalum notatum*, which are recommended for promoting high sporulation (Ijdo et al., 2011; Kumar & Saxena, 2018). However, glomerospores (AMF spores; Goto & Maia, 2006) have hundreds of nuclei that may have genes adapted to a particular host plant species and certain environmental conditions (Kokkoris et al., 2020). Plant and environmental influences occur even during inoculant production in protected environments, reflecting in modifications at the AMF-community level (Sýkorová et al., 2007; Trejo-Aguilar et al., 2013). Therefore, the reduction in

plant survival can be explained by a possible incompatibility between the characteristics incorporated in the inoculant and those present in the target plant and ecosystem of inoculation. This fact is reinforced when considering that the AMF-plant interaction responds to local adaptation (Bauer et al., 2020; Revillini et al., 2016; Rúa et al., 2016). Thus, inoculant production through trap culture may be an alternative to preserve this compatibility by making simple choices such as using soil from reference ecosystems, mixed or not with washed sand, and using it to grow native species (Kozioł et al., 2018). This technique represents an important strategy to investigate the response of plants used in restoration projects.

Here, we investigate how plant soil feedback is influenced by modifications in AMF communities due to choices of soil origin and host plants. Based on studies of AMF application for ecological restoration, we tested whether inoculant production closer to the environmental conditions of a degraded ecosystem can result in positive PSF for plants growing on a similar degraded soil. To this end, soils from reference ecosystems (remnant vegetation and restored area) were grown with *Sorghum bicolor* (widely used for inoculant production) or *Senna uniflora* (a native plant utilized to restore ecosystem). Thereafter, we evaluated how the changes caused by these plants in AMF communities influence the feedback between plant and soil for four herbaceous species used in the restoration of degraded areas (*S. uniflora*, *Mesospharum suaveolens*, *Rhaphiodon echinus* and *Sida galherensis*). Specifically, we tested the following hypotheses:

1. The use of *S. uniflora* for arbuscular mycorrhizal inoculant production is more efficient in promoting biomass accumulation for itself, resulting in positive PSF.
2. Native inoculants cultivated in environmental conditions similar to those found in the field promote greater gain of plant biomass compared to inoculants composed of a mixture of isolates of different AMF species.
3. Inoculants originated from recovered areas promote greater accumulation of plant biomass than those from the remaining vegetation area, because they are composed of AMF tolerant to the soil conditions where they are to be applied.
4. The structure of AMF communities differs due to different soil origins, but also due to the influence of host plant growth.
5. Plants with a lower percentage of mycorrhizal colonization invest more in functional traits related to the rapid acquisition of resources, compensating for the absence or low intensity of mutualistic interaction.

2 | MATERIALS AND METHODS

2.1 | Study system

Our study investigates the interaction between four species of herbaceous plants used in the recovery of degraded areas and AMF communities from soils under influence of the Integration Project of

the São Francisco River with Watersheds of the Northern Northeast (PISF, acronym in Portuguese). Our study was part of environmental installation licences number 438/2007 and 925/2013, ethical approval was not required. The building process required vegetational suppression, followed by mineral extraction, excavation, drilling, and construction of canals to transport water for about 12 million people.

The structure was installed in the Brazilian semiarid region in the largest seasonally dry tropical forest ecosystem in South America, called Caatinga, with low water availability and high solar radiation (Silva et al., 2017). The vegetation composition varies mainly according to the aridity index (Silva & Souza, 2018) and species have adaptations such as water and energy storage in the roots or stem, as well as the loss of leaves in the dry season (Moro et al., 2015). The climate is classified as hot semi-arid, according to Köppen, with mean annual temperatures ranging between 23.4 and 24.8°C, with maximum between 30.4 and 31.4°C and minimum between 18.9 and 19.8°C. Mean annual rainfall indices are between 541 and 627 mm, concentrated between the months of December and April.

2.2 | Soil conditioning phase—Do soil origin and host plant identity modify AMF communities?

We established an experiment to investigate whether AMF sporulation is influenced by the origin of the soil inoculum collected from degraded areas that have been restored (quarry) or from areas of remaining vegetation (Caatinga); as well as by the host plant species (*Sorghum bicolor* and *Senna uniflora*), totaling four treatments, combined factorially, with three repetitions, resulting in 12 experimental units (Figure 1). The first soil origin, Quarry ($n = 15$), comprises rhizospheric soil of *Senna uniflora*, one of the herbaceous species used to restore areas adjacent to the water transport canal. Such areas were severely degraded after mineral exploration activities which exposed the soil to environmental weathering; consequently, erosion processes occurred, leading to a loss in nutrients and organic matter via lixiviation. As a consequence, soil compaction increased, accompanied by a reduction in aeration and water infiltration. The second soil origin, Caatinga ($n = 20$), corresponds to areas of remnant vegetation, neighbouring the areas directly degraded by PISF activities. Before setting up the experiment, the soil samples were dried at room temperature (~22°C) and characterized for physical, chemical (see Appendix S1 and Table S2), and AMF-community parameters (see Appendix S2 and Table S4). Another portion of the soil samples was homogenized according to origin, sieved (2-cm mesh), diluted in previously disinfected sand (1:1 v/v) and distributed in 900 ml pots in the respective treatments. The sand was washed with water and kept in sodium hypochlorite solution (1:0.01 w/v) for 24 h and then washed with water and dried in an oven at 105°C. The seeds of the host plant species were arranged on the soil surface and covered with a thin layer of substrate. After emergence, thinning was performed to keep four individuals per pot. The

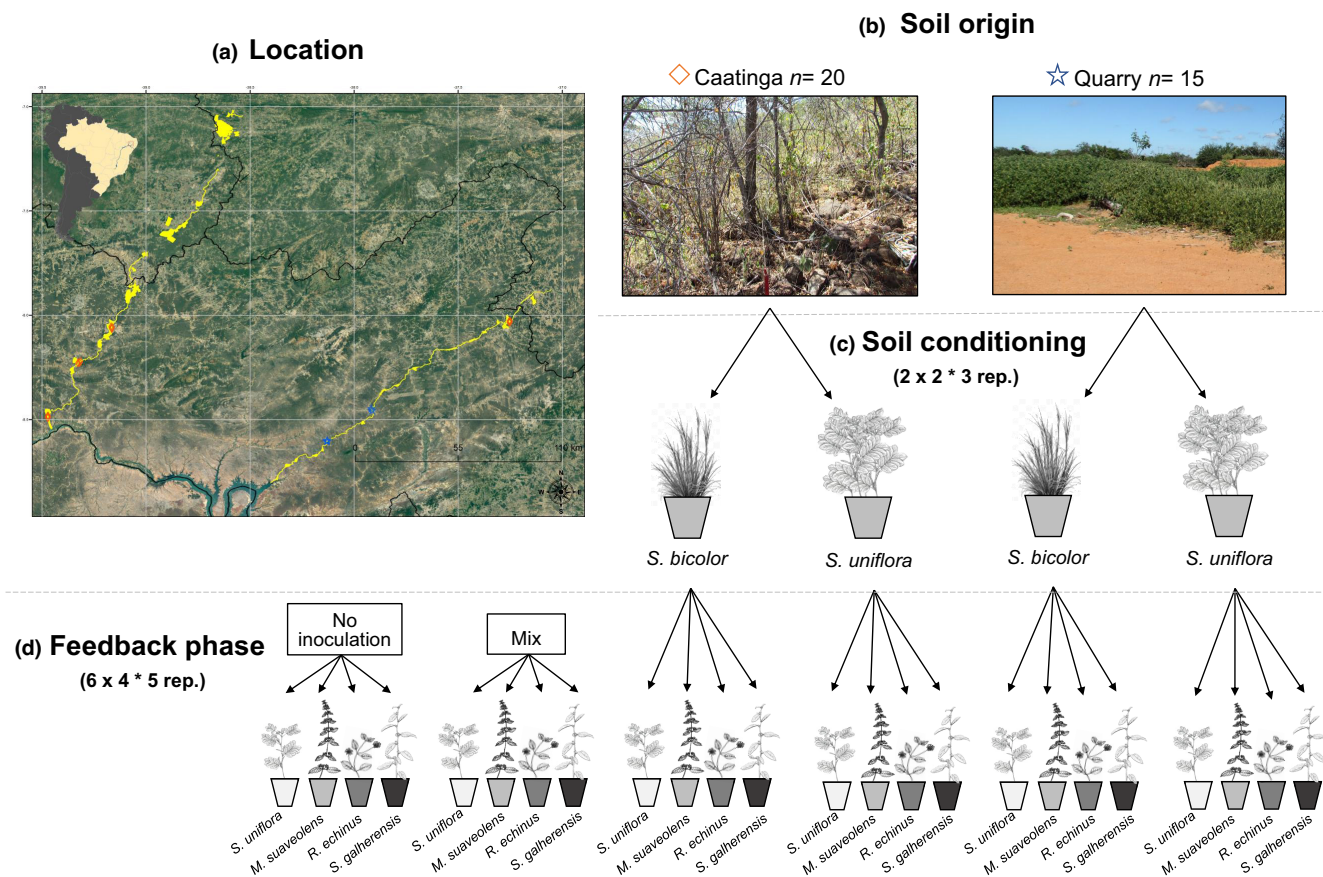


FIGURE 1 Experimental scheme illustrating location (a), the two soil origins (b) (Caatinga and quarry). In the soil conditioning phase (c), we prepared an experiment with a fully randomized design with a factorial arrangement of 2 (soil origin) × 2 (host plant—*Sorghum bicolor* and *Senna uniflora*) in three repetitions ($N = 12$). Thereafter, in the feedback phase (d), we conducted an experiment with randomized block design in factorial arrangement of 6 (inoculants) × 4 (plant species), with five repetitions ($N = 120$). We tested how soil conditioning influences the response of herbaceous species native to the Brazilian semiarid region growing in a background soil collected from an un-restored quarry. The soils inoculum produced in the conditioning phase were contrasted with a treatment containing plants without inoculation (control) and plants inoculated with a mix of AMF isolates tested on other native plants.

plants were irrigated daily with 100 ml of water and maintained for 135 days in a greenhouse at the UNIVASF Campus of Agricultural Sciences (9°19'31.93"S, 40°33'34.24"W) (Figure S3). At the end of the experiment, counting of the number of glomerospores and the identification of AMF species were done from 20-g samples (Figure S1), according to the procedures described in Appendix S2.

2.3 | Feedback phase—Do changes caused in the soil alter performance of herbaceous plants?

We set up the second experiment to test whether the growth of four herbaceous plant species is influenced by the AMF communities originated from two soil (Figure 1), modified by two host plants (conditioning phase). We performed an experiment in a randomized block design in a factorial arrangement with six treatments of inoculation and four herbaceous plants, with five replicates, totalling 120 growing pots. Four inoculants originated from the soil conditioning phase were contrasted with two other treatments, a non-sterilized control (soil without inoculation), and a soil inoculated with

a mixture of three AMF isolates, composed of 100 glomerospores of each of the following isolates: *Acaulospora longula* (URM FMA 07), *Claroideoglossum etunicatum* (Univafsf 05) and *Rhizoglossum intraradices* (CICG-FRA130A), made available from the Culture Collection of Univasf.

To represent a closer condition to the field, we filled the experimental pots (3.0-L) with soil collected from one of the degraded areas by mineral exploration activities (Quarry) at the PISF construction site in the municipality of Floresta, Pernambuco (8°28'16.56"S, 37°54'26.95"W). The soil presented a low abundance of glomerospores (0.46 glomerospores g^{-1} soil) (Table S3). Before setting up the experiment, the soil was homogenized but not sterilized, and fragments above 4 cm were removed.

In the centre of each pot (18 cm diameter × 14 cm high), a portion of soil was removed and filled with a layer of inoculant (soil inoculum). Just above it, 20 seeds and a thin layer of soil were arranged. The weight of each inoculant for each pot was standardized to receive 300 glomerospores (Table 1). After emergence, the seedlings were thinned to maintain one plant per pot, irrigated with 80 ml of water daily during 90 days in a greenhouse.

TABLE 1 Chemical characterization of the substrate after the addition of soil inoculum used in the feedback phase. The soil inoculum was weighed for each pot to reach 300 glomerospores

Origin	Host	Weight (g)	pH	EC	Na	Al	Ca	Mg	K	P
Control	—	—	4.38	0.68	0.70	0.55	2.86	0.90	0.13	0.97
AMF mix	<i>Sorghum bicolor</i>	12	4.46	0.64	0.57	0.65	2.70	0.22	0.13	0.61
Caatinga	<i>Sorghum bicolor</i>	21	4.55	0.61	0.61	0.55	3.52	0.76	0.13	1.05
Caatinga	<i>Senna uniflora</i>	50	4.57	0.60	0.52	0.45	3.15	0.39	0.10	0.68
Quarry	<i>Sorghum bicolor</i>	31	4.62	0.63	0.57	0.15	2.92	0.59	0.10	0.53
Quarry	<i>Senna uniflora</i>	189	4.68	0.55	0.74	0.10	3.47	0.58	0.13	0.53

Note: pH (1:2.5), EC (dS m⁻¹); Na, K, Al, Ca e Mg (cmolc dm⁻³); P (mg dm⁻³).

The four plant species tested in the feedback phase have a wide distribution in the Brazilian semiarid region and have been used in the recovery program of degraded areas of the PISF (Socolowski et al., 2021). The plants are (1) *Senna uniflora* (Mill.) Irwin & Barneby (Fabaceae) which has no records of symbiosis with nitrogen-fixing bacteria (Tedersoo et al., 2018), (2) *Rhaphiodon echinus* (Nees & Mart.) Schauer (Lamiaceae), (3) *Mesosphaerum suaveolens* (L.) Kuntze (Lamiaceae); and (4) *Sida galherensis* Ulbr. (Malvaceae) (Appendix S3; Figure S2).

2.4 | Functional traits and plant parameters

We investigated whether mycorrhizal colonization explains variation in data on functional traits related to resource acquisition and plant biomass allocation (see Appendix S4 for extended methodology). We measured root colonization percentage (Phillips & Hayman, 1970—modified, Giovannetti & Mosse, 1980), the ratio of biomass allocated to roots and shoots (Root:Shoot) (Markestijn & Poorter, 2009), relative growth rate (RGR), specific leaf area (SLA), specific root length (SRL) (Cornelissen et al., 2003, Pérez-Harguindeguy et al., 2016; see Table S6 for calculations).

2.5 | Plant–soil feedback calculations

Two plant–soil feedback (PSF) indices were calculated, using the total dry biomass of plants per experimental block ($n = 5$). We calculated these indexes as proposed by Brinkman et al. (2010):

$$\text{PSF} = \ln \left(\frac{\text{total dry biomass of plant X}}{\text{total dry biomass of plant Y}} \right),$$

where the PSF index assessing plant responses against non-inoculated control corresponds to the value of the inoculated plant (X) divided by the value of the plant without inoculation (Y), and the PSF index assessing plant responses against inoculated control, corresponds to the value of the inoculated plant (X), divided by the value of the plant with the inoculant mix (Y). In cases where the plant without inoculation or plants with inoculant mix were dead, we drew plants from other blocks for the calculation.

2.6 | Statistical analyses

Differences between the structures of AMF communities (Bray–Curtis dissimilarity) from different soil origins and different host plants (soil-conditioning phase) were tested using permutational multi-variate analysis of variance (PERMANOVA), running the `adonis()` function in the 'VEGAN' package (Oksanen et al., 2015) in R software version 3.6.1 (R Core Team, 2019). Communities were also characterized by Shannon–Wiener's diversity index, total richness, glomerospores abundance and Pielou's evenness index (Pielou, 1975). In addition, we investigated whether there were any indicator species of the origin of soil or host plants, using the `multipatt()` function in the 'INDICESPECIES' package (De Caceres & Legendre, 2009).

For the feedback phase, we fitted linear mixed models (LMM) using the plant–soil feedback indices as response variables as a function of the interaction between inoculation treatments and herbaceous species, both considered with fixed effect, while the blocks as random effect. A second set of LMMs was fitted aiming to evaluate how the interaction between root colonization by AMF and herbaceous species affects the measures of PSF, Root:Shoot, SLA and SRL. LMMs were fitted with the respective response variables as a function of species with fixed effects, while blocks were included with random effects. We considered these LMMs with normal error structure of the residuals after graphical analysis of the model variances (Figure S3). We tested the significance of the colonization and species factors using the `Anova()` function available in the 'CAR' package with the prior models (Fox & Weisberg, 2019). All models were tested using the 'LME4' package (Bates et al., 2015) and the `lme()` functions for the LMMs in R software.

3 | RESULTS

3.1 | Soil origin and host plant influence AMF communities

The components of AMF community diversity were affected by the treatments. While the choice of soil origin affected species richness, the choice of host plant affected the evenness of the AMF communities (Table 2). The structure of AMF communities showed significant differences between soil origin ($df = 1$; $R^2 = 0.065$; $p = 0.0002$,

TABLE 2 Diversity, total evenness, total richness and mean of glomerospores count (20g soil^{-1} ; $n = 3$) of the AMF communities recorded after the conditioning phase. Soils were sourced from two reference ecosystems (Caatinga and quarry) and conditioned under the rhizosphere of two plant species (*Senna uniflora* and *Sorghum bicolor*) after 135 days in a greenhouse

	Caatinga		Quarry	
	<i>S. uniflora</i>	<i>S. bicolor</i>	<i>S. uniflora</i>	<i>S. bicolor</i>
Diversity ^a	2.68	1.18	1.24	0.06
Evenness ^b	0.94	0.38	0.89	0.09
Richness	18	22	4	2
Glomerospores	129.7±42.1	304.3±158.2	31.5±10.8	180.0±86.2

^aShannon-Weaver index.

^bPielou index.

Table S7), plant host ($df = 1$; $R^2 = 0.046$; $p = 0.0004$, Table S7) and their interaction ($df = 1$; $R^2 = 0.026$; $p = 0.0156$, Table S7). Soil conditioned by *S. uniflora* showed a more even AMF community. Regardless of host plant identity, the soil originating from Caatinga presented AMF communities with the highest richness (30 species), 26 species more than recorded in the quarry (4 species) (Table 2; Table S4).

Glomus cubense is an indicator species of soil originated from Quarry (Table 3), although it was not found sporulating in the field soil (Table S4). The indicator analysis also showed that *Acaulospora* sp2 is an indicator of soil constrained by *Sorghum bicolor*, and *Septoglomus furcatum* is an indicator of soil constrained by *Senna uniflora*. For the soil originated from Caatinga no indicator species was found (Table 3).

3.2 | Soil inoculum conditioned by *Senna uniflora* leads to positive feedbacks for other herbaceous plants

In both calculated feedback indexes, the responses of inoculated plants were significantly different with respect to the host plant used in the conditioning phase, and with respect to the soil inoculum origin (Table S9). An addition of 31% (Quarry origin) and 37% (Caatinga origin) of dry biomass was accumulated in plants inoculated with soil conditioned by *S. uniflora* relative to *S. bicolor*. The highest PSF were recorded in soil conditioned by *S. uniflora*, with soil originating from Quarry for *M. suaveolens* (1.12 ± 0.18 [mean±SD]) and for *S. galherensis* (1.12 ± 1.05 , Figure 2a). Meanwhile, the soil originating from Caatinga showed the highest positive response for *R. echinus* (1.29 ± 0.79 , Figure 2b) and negative response for *S. galherensis* (-1.24 ± 1.61 , Figure 3b) and for *S. uniflora* itself (-0.35 ± 0.64 , Figure 3a).

The herbaceous species tested showed significant differences regarding the intensity of plant-soil feedback (Table S8). Among the species, the greatest response was recorded for *M. suaveolens* (0.62 ± 0.3), a species that benefited from all inoculants tested

TABLE 3 AMF species indicator analysis. IV = indicator value, statistic of the test calculated according to De Caceres and Legendre (2009)

Species	Treatment	IV	p value
<i>Glomus cubense</i>	Quarry	0.376	<0.0001
<i>Acaulospora</i> sp2	<i>Sorghum bicolor</i>	0.303	0.002
<i>Septoglomus furcatum</i>	<i>Senna uniflora</i>	0.254	0.0201

(Figure 2). The opposite occurred in *S. uniflora* and *S. galherensis*, which did not benefit from inoculation, either compared to the control without inoculation (Figure 2a) or the inoculation with the mix of AMF isolates (Figure 2b), except when tested in the soil conditioned by *S. uniflora* originating from the Quarry.

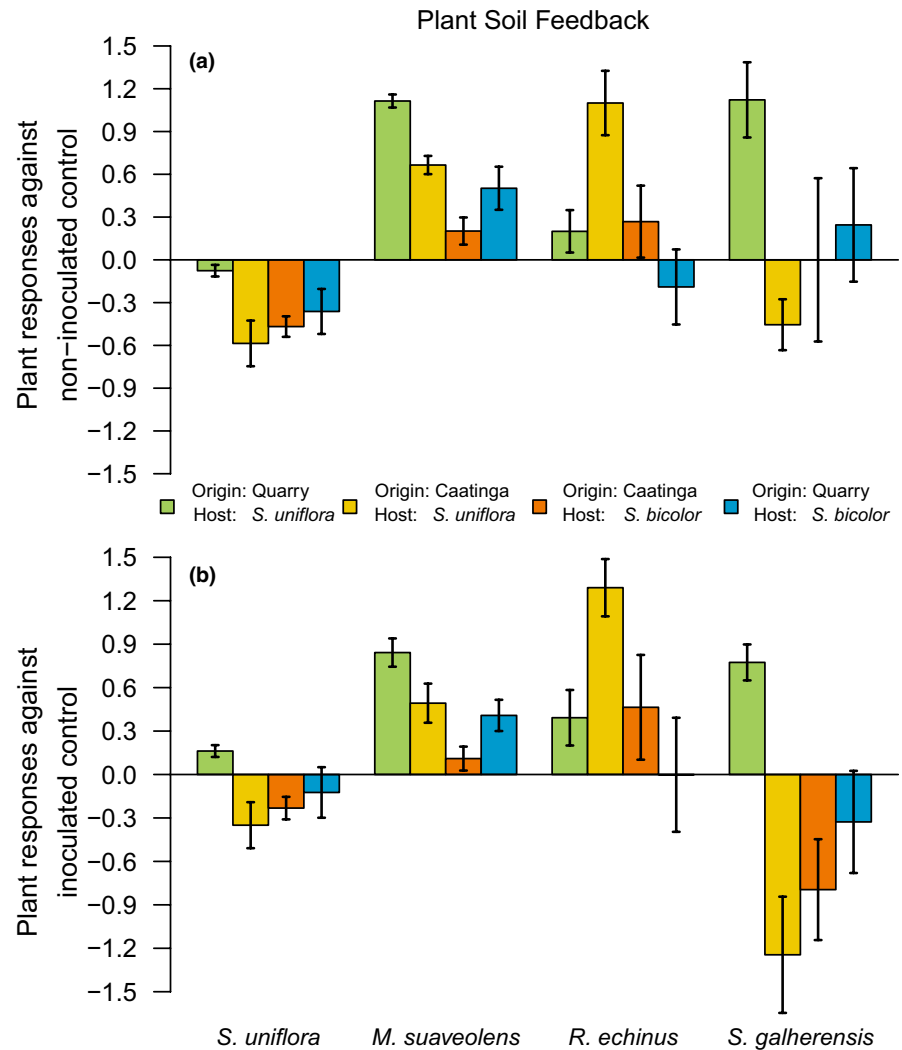
3.3 | Mycorrhizal colonization increases plant-soil feedback and explains variation in plant traits

The plant-soil feedback (PSF) values were positively related to the percentage of root colonization by AMF ($X^2 = 8.9$; $df = 1$; $p = 0.003$). This relationship differed in intensity as a function of the species analysed ($X^2 = 21.9$; $df = 3$; $p < 0.0001$), with *S. galherensis* (0.5 ± 1.3) being the most positively influenced ($coef = 0.94$; $ep = 0.24$; $t = 3.925$), ranging from negative PSF values at low mycorrhizal colonization percentages to positive values when mycorrhizal colonization was high. The same was observed for *R. echinus* (0.3 ± 0.9) and *M. suaveolens* (0.6 ± 0.5) (Figure 3a; Table S7). Most observations of PSF in *S. uniflora* were negative (-0.4 ± 0.4), nevertheless, the species also followed the tendency of recording higher PSF values as a function of increasing colonization percentage (Figure 3a).

Plants allocated more biomass to the roots with increasing root colonization by AMF ($X^2 = 13.4$; $df = 1$; $p = 0.0002$), resulting in positive relationships between root dry biomass and mycorrhizal root colonization (Figure 3b; Table S10). The species showed distinct patterns regarding the ratio of biomass allocated to the root and shoot ($X^2 = 39.9$; $df = 3$; $p < 0.0001$). Most plants of *S. uniflora* favoured root biomass allocation over shoot biomass (1.2 ± 0.4), contrary to what occurred for the other species; the lowest means were recorded in *R. echinus* (0.7 ± 0.3) and *S. galherensis* (0.8 ± 0.4), while *M. suaveolens* (0.9 ± 0.2) showed a proportional mean in biomass allocation (close to 1).

Plants invested more in fine and long roots (higher SRL) in situations of low colonization percentage ($X^2 = 7.9$; $df = 1$; $p = 0.005$). Differences among species were significant with respect to SRL ($X^2 = 18.2$; $df = 3$; $p = 0.0004$), with *S. uniflora* (4391.1 ± 1131.4) being the species that showed thicker and poorly elongated roots. The species *S. galherensis* (5922.7 ± 1264.7) and *M. suaveolens* (6484.3 ± 2745.9) showed relationships between SRL and mycorrhizal root colonization that were similar to each other and stronger when compared to *R. echinus* (6235.8 ± 2061.3) (Figure 3c; Table S10). SRL responded inversely to the relationship between PSF or root to shoot with mycorrhizal root colonization.

FIGURE 2 Plant–soil feedback (PSF) calculated by the log of the ratio of the dry biomass of plants in each inoculation treatment in relation to the dry biomass of non-inoculated plants (control per block), for each of the four species. Positive PSF values without inoculation (a) indicate greater biomass accumulation of the inoculated plant compared to plants without inoculation, while positive PSF values with inoculation (b) indicate greater biomass accumulation compared to plants inoculated with a mixture of AMF isolates (mix). Bars represent mean and whiskers standard error.



Specific leaf area (SLA) showed a negative relationship with mycorrhizal colonization percentage ($X^2 = 3.8$; $df = 1$; $p = 0.05$), with differences among the species studied ($X^2 = 31.1$; $df = 3$; $p < 0.0001$). While *R. echinus* ($coef = -1.10$; $SD = 0.95$; $t = -1.155$) showed a negative relationship between mycorrhizal colonization and SLA; all other species showed weak positive or neutral relationships (Figure 3c; Table S10).

4 | DISCUSSION

We found that the soil inoculum conditioned by *Senna uniflora* increased the biomass of other herbaceous species, but not of itself. With this, we reject our first hypothesis that positive PSF would be recorded in *S. uniflora* inoculated with its own soil inoculum. This result indicates that *S. uniflora* may be an early successional species, probably with low competitor potential, since ruderal plants are often associated with negative PSF (Kardol et al., 2006; Wubs et al., 2019). But it also indicates that *S. uniflora* may create favourable edaphic conditions for other herbaceous species through modification in the AMF community.

Indeed, biomass and height increases tend to be greater when inoculating soil conditioned by other species (Kuřáková et al., 2018). However, we found negative PSF more often in plants inoculated with soil inoculum conditioned by *Sorghum bicolor* compared to *S. uniflora*. Although *S. bicolor* promoted AMF abundance in the soil of recovering Quarry, the communities consistently showed lower evenness compared to *S. uniflora*, corroborating results that *S. bicolor* increases glomerospore density (Bever et al., 1996) and decreases evenness under greenhouse cultivation (Sýkorová et al., 2007). These results reinforce the idea that some plants may benefit more from the AMF community of another coexisting plant species than from itself (Bever, 2002). In this sense, the production and application of soil inoculum conditioned by *S. uniflora* may work to transport AMF communities capable of benefiting herbaceous species in ecological restoration projects in the dry forest of Brazilian semiarid region.

In our study, the soils inoculum of *S. uniflora* and the inoculant mix showed high evenness. However, only the soils inoculum of *S. uniflora* increased plant biomass, while the inoculant mix showed similar results to plants without inoculation, confirming our second hypothesis. In soil, AMF species with higher relative abundance

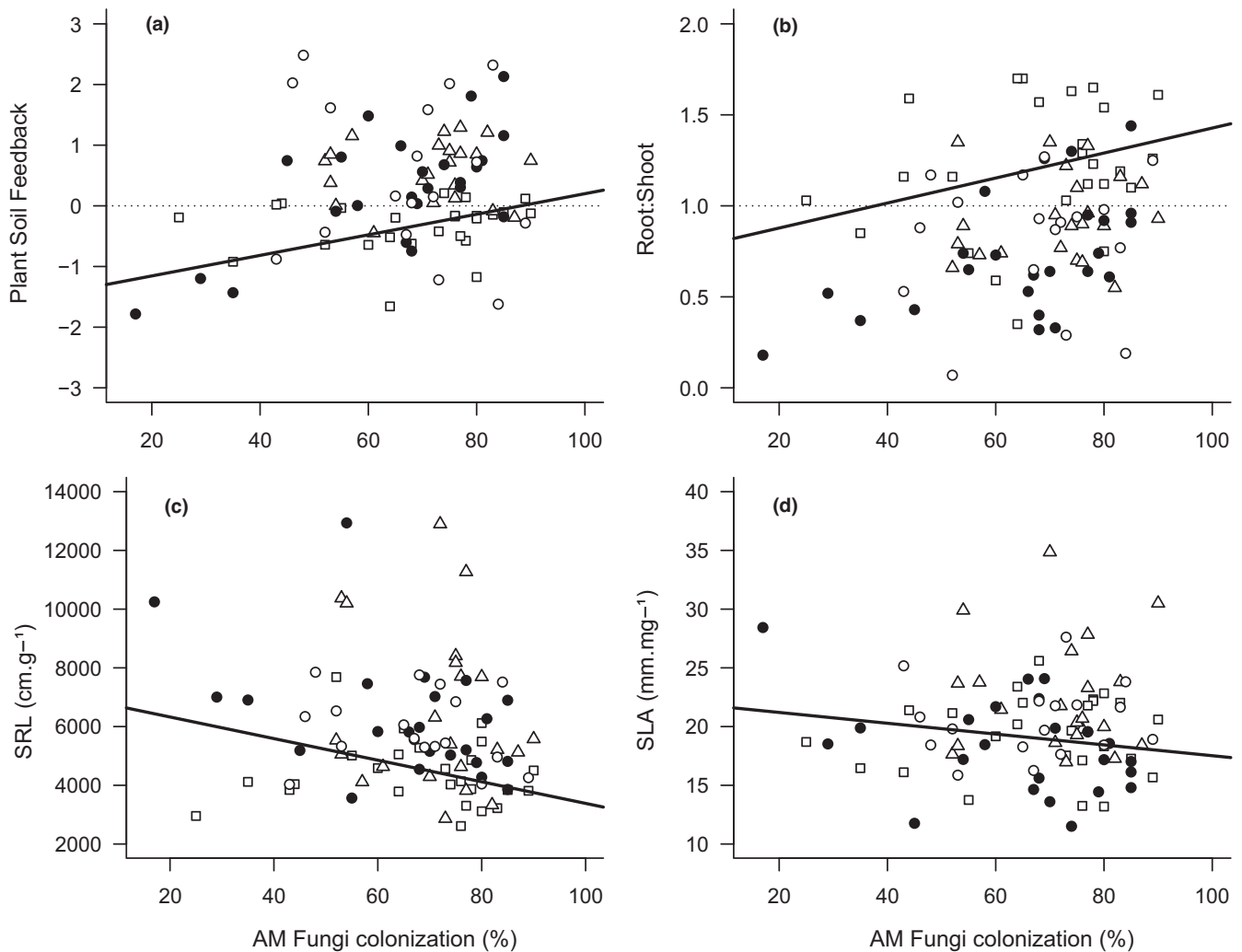


FIGURE 3 Relationship of root colonization by AMF in the (a) plant–soil feedback index, calculated by the log of the ratio between dry biomass of plants in each inoculant and dry biomass of non-inoculated plants (control per block). Values above the dashed line indicate greater biomass accumulation in inoculated plants than in non-inoculated plants, (b) ratio between root and shoot dry weight. Values above the dashed line indicate greater biomass allocation in the root than in the shoot, (c) specific root length (SRL) and (d) specific leaf area (SLA). Symbols indicate species as follows, \square *S. uniflora*, \triangle *M. suaveolens*, \bullet *R. echinus* and \circ *S. galherensis*.

have a greater numerical chance of establishing associations than species with lower relative abundance. However, species differ in glomerospore germination speed and root colonization strategy. For example, Hart and Reader (2002) observed that *Glomus* species (such as *G. cubense*) are faster at colonizing roots than *Acaulospora* species and also show more extensive root colonization. Therefore, the first colonizers tend to dominate and compete for space in the root cortex against species that colonize later, which sets up the priority effect (Werner & Kiers, 2015). Consequently, the functions performed by the dominant species in the root tend to excel. If they are related to plant growth promotion, the PSF values tend to be positive, as observed by Bennett and Bever (2007) and Crossay et al. (2019). The evenness present in the soil inoculum of *S. uniflora* may have decreased the strength of the priority effect and, in addition to the preservation of the local adaptation provided by the adopted methodology, may have allowed AMF with growth-promoting function to colonize the roots of the plant species tested, especially

S. galherensis and *R. echinus*, which showed substantial increments in biomass. Therefore, in the context of ecological restoration, the application of native AMF inoculants with more even communities should be prioritized over inoculants composed of isolates with low adaptation to the inoculation target conditions.

Soil origin influenced the structure of the AMF communities and altered the levels of plant biomass depending on the herbaceous species tested. We can confirm the third hypothesis regarding the AMF community. Certainly, the stressful condition present in the Quarry soil selected stress-tolerant and ruderal species. *Glomus cubense* might be a clear example of a ruderal species, given that it was reported an indicator species of the soil originating from Quarry, and furthermore, this species also showed high sporulation during the soil conditioning phase and might be related to the increased root colonization in the feedback phase. Such characteristics corroborate those reported by Chagnon et al. (2013). Additionally, *G. cubense* has already been related to increased phosphorus concentration in the

tissue of leguminous species (Klabi et al., 2014) and to increased productivity of different agricultural crops such as banana, cassava, and forages in the tropical region (Cañizares et al., 2016). Furthermore, *Paraglomus occultum* can be recognized as an example of stress-tolerant species, because it remained in the soil under different disturbance conditions in our study. This find corroborates previous studies that showed the ability of *P. occultum* to maintain colonization and to promote growth on *Citrus tangerine* even under high salinity (Wu et al., 2010). This species has already been reported under similar stressful conditions in the Brazilian semiarid, such as in areas degraded by limestone (Teixeira-Rios et al., 2013) and gypsum mining (Mergulhão et al., 2010), as well as in areas prone to desertification in the Mediterranean semiarid (Ferrol et al., 2004).

The soil inoculum originating from the area of remaining vegetation showed higher richness and number of glomerospores, compared to soil from the recovering area. This confirms our fourth hypothesis; however, greater richness was not always represented an increase in the PSF. This can be explained by some species were not always associated with increased plant response, such as *Acaulospora morrowiae* (Zanchi et al., 2021), or by species that may be useful for biological control such as *Entrophospora infrequens* in soybean attacked by bacterial pathogens (Malik et al., 2016). Despite these changes in AMF communities, the intensity of PSF varied according to the origin of the inoculant. Several studies have shown the relevance of inoculating soil with native AMF communities rather than commercial inoculants (Maltz & Treseder, 2015; Neuenkamp et al., 2019). Our results suggest that inoculant mix of AMF isolates may not be an alternative to increase plant biomass, diverging from that found by Koziol et al. (2021). Other studies show increased biomass and survival in plants inoculated with soil originating from remnant vegetation (Smith et al., 2018; Wubs et al., 2016). Although the richness of AMF species in Quarry soil inoculum was four species, this set of species favoured a positive PSF in *M. suaveolens*, *S. uniflora* and *S. galherensis* (early successional plants) compared to the AMF community found in the soil inoculum of Caatinga (18 species), reinforcing the proposition by Koziol and Bever (2019) that species composition is more determinant than richness. Since the analysis pointed *G. cubense* as a Quarry soil indicator species, it is possible that it is a key species for productivity. Future studies should be conducted to confirm its role in degraded soils of the Caatinga.

Plants compensated for the low percentage of root colonization by AMF by investing in functional resource acquisition traits, confirming our fifth hypothesis. Our results corroborate the pattern that plants invest less in active soil nutrient searching (lower SRL) when they have a higher colonization percentage (Sweeney et al., 2021). We also found this response for SLA, different from the results found by Semchenko et al. (2018) and Cortois et al. (2016). In general, the plants tested accumulated more biomass in the shoot than in the root, contrary to what is expected, since tree plants in the same study system tend to allocate more biomass in the roots (Teixeira et al., 2020). Certainly, this divergence occurs because they are annual herbaceous plants that tend to invest energy for reproduction in the rainy season. Thus, we expected that plants with

greater mycorrhizal colonization would invest even more biomass in the shoot. However, inoculation with native AMF increased root colonization of the plants, which in turn accumulated more biomass in the roots. This fact may be due to the low nutrient availability (mainly $P = 0.10 \text{ mg dm}^{-3}$) in the background soil, directing the plant-AMF interaction to actively search for nutrients in the soil. This scenario can reflect in benefits for recovery of a degraded soil, as the joint increase in AMF colonization and root production can drive carbon input into the soil (Rillig et al., 2001), promoting the flow of nutrients and energy between different trophic levels (Antunes & Koyama, 2017). In this way, edaphic conditions can be improved by promoting the establishment of other plant species and contributing to successional advancement and the success of ecological restoration programs.

Our study suggests the importance of incorporating strategies to preserve local adaptation during AMF inoculant production aimed at application in restoration projects. Three aspects were considered and corroborated: (1) the predictions of local adaptation of AMF communities, soil and plant (Rúa et al., 2016); (2) the choice of native AMF inoculant instead of commercial or AMF isolates (Maltz & Treseder, 2015); and (3) the establishment of an AMF management model in ecological restoration projects (Asmelash et al., 2016). The success of the adopted strategy was influenced by the choice of cultivation technique (trap culture with native soil instead of AMF isolates), and the host belonging to native flora (*S. uniflora* instead of *S. bicolor*). These decisions may favour the adaptation of the inoculant to those conditions present in the recovery target soil and intensify the accumulation of plant biomass in early successional plants, even in a severely degraded soil.

AUTHOR CONTRIBUTIONS

Adler Santana Medeiros, Adriana Mayumi Yano-Melo and Renato Garcia Rodrigues conceived the ideas; Adler Santana Medeiros, Adriana Mayumi Yano-Melo, Daniela Cristine Mascia Vieira, Fábio Socolowski designed the methodology; Adler Santana Medeiros, Edjane Silva Damasceno and Julie Christine Scaloppi collected the data; Adler Santana Medeiros and Bruno Tomio Goto identified the glomerospores; Adler Santana Medeiros analysed the data; and Adler Santana Medeiros, Edjane Silva Damasceno and Julie Christine Scaloppi led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.qz612jmgm> (Medeiros et al., 2022).

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REFERENCES

- Antunes, P. M., & Koyama, A. (2017). Mycorrhizas as nutrient and energy pumps of soil food webs: Multitrophic interactions and feedbacks. In *Mycorrhizal mediation of soil: Fertility, structure, and carbon storage*. Elsevier Inc. <https://doi.org/10.1016/B978-0-12-804312-7.00009-7>
- Aronson, J., Goodwin, N., Orlando, L., Eisenberg, C., & Cross, A. T. (2020). A world of possibilities: Six restoration strategies to support the united Nation's decade on ecosystem restoration. *Restoration Ecology*, 28(4), 730–736. <https://doi.org/10.1111/rec.13170>
- Asmelash, F., Bekele, T., & Bihane, E. (2016). The potential role of arbuscular mycorrhizal fungi in the restoration of degraded lands. *Frontiers in Microbiology*, 7(1095), 1–15. <https://doi.org/10.3389/fmicb.2016.01095>
- Bates, D., Kliegl, R., Vasishth, S., & Baayen, H. (2015). Parsimonious mixed models. *arXiv: Methodology*. <http://arxiv.org/abs/1506.04967>
- Bauer, J. T., Koziol, L., & Bever, J. D. (2020). Local adaptation of mycorrhizae communities changes plant community composition and increases aboveground productivity. *Oecologia*, 192, 735–744. <https://doi.org/10.1007/s00442-020-04598-9>
- Bennett, A. E., & Bever, J. D. (2007). Mycorrhizal species differentially alter plant growth and response to herbivory. *Ecology*, 88(1), 210–218. [https://doi.org/10.1890/0012-9658\(2007\)88\[210:MSDAPG\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[210:MSDAPG]2.0.CO;2)
- Bennett, J. A., & Klironomos, J. (2019). Mechanisms of plant–soil feedback: Interactions among biotic and abiotic drivers. *New Phytologist*, 222(1), 91–96. <https://doi.org/10.1111/nph.15603>
- Bever, J. D. (2002). Negative feedback within a mutualism: Host-specific growth of mycorrhizal fungi reduces plant benefit. *Proceedings of the Royal Society B: Biological Sciences*, 269(1509), 2595–2601. <https://doi.org/10.1098/rspb.2002.2162>
- Bever, J. D., Dickie, I. A., Facelli, E., Facelli, J. M., Klironomos, J., Moora, M., Rillig, M. C., Stock, W. D., Tibbett, M., & Zobel, M. (2010). Rooting theories of plant community ecology in microbial interactions. *Trends in Ecology & Evolution*, 25(8), 468–478. <https://doi.org/10.1016/j.tree.2010.05.004>
- Bever, J. D., Morton, J. B., Antonovics, J., & Schultz, P. A. (1996). Host-dependent sporulation and species diversity of arbuscular mycorrhizal fungi in a mown grassland. *The Journal of Ecology*, 84(1), 71–82. <https://doi.org/10.2307/2261701>
- Bever, J. D., Westover, K. M., & Antonovics, J. (1997). Incorporating the soil community into plant population dynamics: The utility of the feedback approach. *Journal of Ecology*, 85(5), 561–573. <https://doi.org/10.2307/2960528>
- Brinkman, E. P., Van der Putten, W. H., Bakker, E. J., & Verhoeven, K. J. F. (2010). Plant–soil feedback: Experimental approaches, statistical analyses and ecological interpretations. *Journal of Ecology*, 98(5), 1063–1073. <https://doi.org/10.1111/j.1365-2745.2010.01695.x>
- Cañizares, P. J. G., Pedroso, J. F. R., Espinosa, R. R., Jiménez, A. H., & Flores, G. C. (2016). Efectividad de la inoculación de hongos micorrizicos arbusculares en dos leguminosas forrajeras cultivadas en dos tipos de suelo. *Tropical Grasslands-Forrajeras Tropicales*, 4(2), 82–90. [https://doi.org/10.17138/tgft\(4\)82-90](https://doi.org/10.17138/tgft(4)82-90)
- Chagnon, P. L., Bradley, R. L., Maherali, H., & Klironomos, J. N. (2013). A trait-based framework to understand life history of mycorrhizal fungi. *Trends in Plant Science*, 18(9), 484–491. <https://doi.org/10.1016/j.tplants.2013.05.001>
- Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., ter Steege, H., Morgan, H. D., van der Heijden, M. G. A., Pausas, J. G., & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51(4), 335–380. <https://doi.org/10.1071/BT02124>
- Cortois, R., Schröder-Georgi, T., Weigelt, A., van der Putten, W. H., & De Deyn, G. B. (2016). Plant–soil feedbacks: Role of plant functional group and plant traits. *Journal of Ecology*, 104(6), 1608–1617. <https://doi.org/10.1111/1365-2745.12643>
- Crossay, T., Majorel, C., Redecker, D., Gensous, S., Medevielle, V., Durrieu, G., Cavaloc, Y., & Amir, H. (2019). Is a mixture of arbuscular mycorrhizal fungi better for plant growth than single-species inoculants? *Mycorrhiza*, 29(4), 325–339. <https://doi.org/10.1007/s00572-019-00898-y>
- De Caceres, M., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, 90(12), 3566–3574. <https://doi.org/10.1890/08-1823.1>
- Eissenstat, D. M., Kucharski, J. M., Zadworny, M., Adams, T. S., & Koide, R. T. (2015). Linking root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate forest. *New Phytologist*, 208(1), 114–124. <https://doi.org/10.1111/nph.13451>
- Ferrol, N., Calvente, R., Cano, C., Barea, J. M., & Azcón-Aguilar, C. (2004). Analysing arbuscular mycorrhizal fungal diversity in shrub-associated resource islands from a desertification-threatened semi-arid Mediterranean ecosystem. *Applied Soil Ecology*, 25(2), 123–133. <https://doi.org/10.1016/j.apsoil.2003.08.006>
- Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage. <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>
- Francioli, D., van Rijssel, S. Q., van Ruijven, J., Termorshuizen, A. J., Cotton, T. E. A., Dumbrell, A. J., Raaijmakers, J. M., Weigelt, A., & Mommer, L. (2021). Plant functional group drives the community structure of saprophytic fungi in a grassland biodiversity experiment. *Plant and Soil*, 461(1–2), 91–105. <https://doi.org/10.1007/s11104-020-04454-y>
- Giovannetti, M., & Mosse, B. (1980). An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. *New Phytologist*, 84(3), 489–500.
- Goto, B. T., & Maia, L. C. (2006). Glomerospores: A new denomination for the spores of Glomeromycota, a group molecularly distinct from the Zygomycota. *Mycotaxon*, 96(4), 129–132.
- Hart, M. M., & Reader, R. J. (2002). Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. *New Phytologist*, 153(2), 335–344. <https://doi.org/10.1046/j.0028-646X.2001.00312.x>
- Hoeksema, J. D., Chaudhary, V. B., Gehring, C. A., Johnson, N. C., Karst, J., Koide, R. T., Pringle, A., Zabinski, C., Bever, J. D., Moore, J. C., Wilson, G. W. T., Klironomos, J. N., & Umbanhowar, J. (2010). A

- meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters*, 13(3), 394–407. <https://doi.org/10.1111/j.1461-0248.2009.01430.x>
- Ijdo, M., Cranenbrouck, S., & Declerck, S. (2011). Methods for large-scale production of AM fungi: Past, present, and future. *Mycorrhiza*, 21(1), 1–16. <https://doi.org/10.1007/s00572-010-0337-z>
- Kardol, P., Bezemer, T. M., & Van Der Putten, W. H. (2006). Temporal variation in plant-soil feedback controls succession. *Ecology Letters*, 9(9), 1080–1088. <https://doi.org/10.1111/j.1461-0248.2006.00953.x>
- Klabi, R., Hamel, C., Schellenberg, M. P., Iwaasa, A., Raies, A., & St-Arnaud, M. (2014). Interaction between legume and arbuscular mycorrhizal fungi identity alters the competitive ability of warm-season grass species in a grassland community. *Soil Biology and Biochemistry*, 70, 176–182. <https://doi.org/10.1016/j.soilbio.2013.12.019>
- Kokkoris, V., Stefani, F., Dalpé, Y., Dettman, J., & Corradi, N. (2020). Nuclear dynamics in the arbuscular mycorrhizal fungi. *Trends in Plant Science*, 25(8), 765–778. <https://doi.org/10.1016/j.tplan.2020.05.002>
- Koziol, L., Bauer, J. T., Duell, E. B., Hickman, K., House, G. L., Schultz, P. A., Tipton, A. G., Wilson, G. W. T., & Bever, J. D. (2021). Manipulating plant microbiomes in the field: Native mycorrhizae advance plant succession and improve native plant restoration. *Journal of Applied Ecology*, 59(January), 1–10. <https://doi.org/10.1111/1365-2664.14036>
- Koziol, L., & Bever, J. D. (2019). Mycorrhizal feedbacks generate positive frequency dependence accelerating grassland succession. *Journal of Ecology*, 107(2), 622–632. <https://doi.org/10.1111/1365-2745.13063>
- Koziol, L., Schultz, P. A., House, G. L., Bauer, J. T., Middleton, E. L., & Bever, J. D. (2018). The plant microbiome and native plant restoration: The example of native mycorrhizal fungi. *BioScience*, 68(12), 996–1006. <https://doi.org/10.1093/biosci/biy125>
- Kumar, M., & Saxena, A. K. (2018). Conventional methods for mass multiplication of AMF. In *Mycorrhiza—Nutrient uptake, biocontrol, ecorestoration* (4th ed., pp. 287–300). https://doi.org/10.1007/978-3-319-68867-1_15
- Kutáková, E., Herben, T., & Münzbergová, Z. (2018). Heterospecific plant–soil feedback and its relationship to plant traits, species relatedness, and co-occurrence in natural communities. *Oecologia*, 187(3), 679–688. <https://doi.org/10.1007/s00442-018-4145-z>
- Malik, R. J., Dixon, M. H., & Bever, J. D. (2016). Mycorrhizal composition can predict foliar pathogen colonization in soybean. *Biological Control*, 103, 46–53. <https://doi.org/10.1016/j.biocontrol.2016.08.004>
- Maltz, M. R., & Treseder, K. K. (2015). Sources of inocula influence mycorrhizal colonization of plants in restoration projects: A meta-analysis. *Restoration Ecology*, 23(5), 625–634. <https://doi.org/10.1111/rec.12231>
- Markesteijn, L., & Poorter, L. (2009). Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought and shade-tolerance. *Journal of Ecology*, 97(2), 311–325. <https://doi.org/10.1111/j.1365-2745.2008.01466.x>
- McCormack, M. L., & Iversen, C. M. (2019). Physical and functional constraints on viable belowground acquisition strategies. *Frontiers in Plant Science*, 10(October), 1–12. <https://doi.org/10.3389/fpls.2019.01215>
- Medeiros, A. S., Scaloppi, J. C., Damasceno, E. S., Goto, B. T., Vieira, D. C. M., Socolowski, F., Rodrigues, R. G., & Yano-Melo, A. M. (2022). Data from: Arbuscular mycorrhizal fungi communities shaped by host-plant affect the outcome of plant–soil feedback in dryland restoration. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.qz612jmgm>
- Mergulhão, A. C. E. S., Burity, H. A., Goto, B. T., & Maia, L. C. (2010). Diversity of arbuscular mycorrhizal fungi in a gypsum mining impacted semiarid area. *Acta Botânica Brasileira*, 24(4), 1052–1061. <https://doi.org/10.1590/s0102-33062010000400020>
- Moro, M. F., Macedo, M. B., de Moura-Fé, M. M., Farias Castro, A. S., & da Costa, R. C. (2015). Vegetação, unidades fitoecológicas e diversidade paisagística do estado do Ceará. *Rodriguesia*, 66(3), 717–743. <https://doi.org/10.1590/2175-7860201566305>
- Neuenkamp, L., Prober, S. M., Price, J. N., Zobel, M., & Standish, R. J. (2019). Benefits of mycorrhizal inoculation to ecological restoration depend on plant functional type, restoration context and time. *Fungal Ecology*, 40, 140–149. <https://doi.org/10.1016/j.funeco.2018.05.004>
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. (2015). *Vegan: Community ecology package*. R Package Version 2.5-7. <http://CRAN.R-project.org/package=vegan>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., ... Cornelissen, J. H. C. (2016). Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 64(8), 715–716. https://doi.org/10.1071/BT12225_CO
- Phillips, J. M., & Hayman, D. S. (1970). Improved procedures for clearing roots and staining parasitic and vesicular mycorrhizal fungi for rapid assessment of infection. *Transactions of the British Mycological Society*, 55, 58–161. [https://doi.org/10.1016/S0007-1536\(70\)80110-3](https://doi.org/10.1016/S0007-1536(70)80110-3)
- Pielou, E. C. (1975). *Ecological diversity*. Wiley, Universidade de Michigan.
- Piñeiro, J., Maestre, F. T., Bartolomé, L., & Valdecantos, A. (2013). Ecotechnology as a tool for restoring degraded drylands: A meta-analysis of field experiments. *Ecological Engineering*, 61, 133–144. <https://doi.org/10.1016/j.ecoleng.2013.09.066>
- Powell, J. R., & Rillig, M. C. (2018). Biodiversity of arbuscular mycorrhizal fungi and ecosystem function. *New Phytologist*, 220(4), 1059–1075. <https://doi.org/10.1111/nph.15119>
- R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Reinhardt, D. R., & Miller, R. M. (1990). Size classes of root diameter and mycorrhizal fungal colonization in two temperate grassland communities. *New Phytologist*, 116(1), 129–136. <https://doi.org/10.1111/j.1469-8137.1990.tb00518.x>
- Revillini, D., Gehring, C. A., & Johnson, N. C. (2016). The role of locally adapted mycorrhizas and rhizobacteria in plant–soil feedback systems. *Functional Ecology*, 30(7), 1086–1098. <https://doi.org/10.1111/1365-2435.12668>
- Rillig, M. C., Wright, S. F., Nichols, K. A., Schmidt, W. F., & Torn, M. S. (2001). Large contribution of arbuscular mycorrhizal fungi to soil carbon pools in tropical forest soils. *Plant and Soil*, 233(2), 167–177. <https://doi.org/10.1023/A:1010364221169>
- Rodríguez, R., & Durán, P. (2020). Natural rhizobiome engineering by using native extreme microbiome to counteract the climate change effects. *Frontiers in Bioengineering and Biotechnology*, 8(June), 1–14. <https://doi.org/10.3389/fbioe.2020.00568>
- Rúa, M. A., Antoninka, A., Antunes, P. M., Chaudhary, V. B., Gehring, C., Lamit, L. J., Piculell, B. J., Bever, J. D., Zabinski, C., Meadow, J. F., Lajeunesse, M. J., Milligan, B. G., Karst, J., & Hoeksema, J. D. (2016). Home-field advantage? Evidence of local adaptation among plants, soil, and arbuscular mycorrhizal fungi through meta-analysis. *BMC Evolutionary Biology*, 16(122), 1–15. <https://doi.org/10.1186/s12862-016-0698-9>
- Semchenko, M., Leff, J. W., Lozano, Y. M., Saar, S., Davison, J., Wilkinson, A., Jackson, B. G., Pritchard, W. J., De Long, J. R., Oakley, S., Mason,

- K. E., Ostle, N. J., Baggs, E. M., Johnson, D., Fierer, N., & Bardgett, R. D. (2018). Fungal diversity regulates plant-soil feedbacks in temperate grassland. *Science Advances*, 4(11), 1–9. <https://doi.org/10.1126/sciadv.aau4578>
- Silva, A. C., & Souza, A. F. (2018). Aridity drives plant biogeographical sub regions in the Caatinga, the largest tropical dry forest and woodland block in South America. *PLoS ONE*, 13(4), 1–22. <https://doi.org/10.1371/journal.pone.0196130>
- Silva, J. C., Leal, I., & Tabarelli, M. (2017). *Caatinga: The largest tropical dry forest region in South America* (1st ed.). Springer.
- Smith, M. E., Delean, S., Cavagnaro, T. R., & Facelli, J. M. (2018). Evidence for species-specific plant responses to soil microbial communities from remnant and degraded land provides promise for restoration. *Austral Ecology*, 43(3), 301–308. <https://doi.org/10.1111/aec.12567>
- Socolowski, F., Vieira, D. C. M., Souza, B. R., Melo, F. P. L., & Rodrigues, R. G. (2021). Restoration in Caatinga: A proposal for revegetation methods for the most exclusive and least known ecosystem in Brazil. *Multequina—Latin American Journal of Natural Resources*, 30(2), 247–263.
- Swanson, M. E., Franklin, J. F., Beschta, R. L., Crisafulli, C. M., DellaSala, D. A., Hutto, R. L., Lindenmayer, D. B., & Swanson, F. J. (2011). The forgotten stage of forest succession: Early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, 9(2), 117–125. <https://doi.org/10.1890/090157>
- Sweeney, C. J., de Vries, F. T., van Dongen, B. E., & Bardgett, R. D. (2021). Root traits explain rhizosphere fungal community composition among temperate grassland plant species. *New Phytologist*, 229(3), 1492–1507. <https://doi.org/10.1111/nph.16976>
- Sýkorová, Z., Ineichen, K., Wiemken, A., & Redecker, D. (2007). The cultivation bias: Different communities of arbuscular mycorrhizal fungi detected in roots from the field, from bait plants transplanted to the field, and from a greenhouse trap experiment. *Mycorrhiza*, 18, 1–14. <https://doi.org/10.1007/s00572-007-0147-0>
- Tedersoo, L., Laanisto, L., Rahimlou, S., Toussaint, A., Hallikma, T., & Pärtel, M. (2018). Global database of plants with root-symbiotic nitrogen fixation: NodDB. *Journal of Vegetation Science*, 29(3), 560–568. <https://doi.org/10.1111/jvs.12627>
- Teixeira, L. H., Oliveira, B. F., Krahe, F. S., Kollmann, J., & Ganade, G. (2020). Linking plant traits to multiple soil functions in semi-arid ecosystems. *Journal of Arid Environments*, 172, 104040. <https://doi.org/10.1016/j.jaridenv.2019.104040>
- Teixeira-Rios, T., de Souza, R. G., Maia, L. C., Oehl, F., & Lima, C. E. P. (2013). Arbuscular mycorrhizal fungi in a semi-arid, limestone mining-impacted area of Brazil. *Acta Botanica Brasilica*, 27(4), 688–693. <https://doi.org/10.1590/S0102-33062013000400006>
- Trejo-Aguilar, D., Lara-Capistrán, L., Maldonado-Mendoza, I. E., Zulueta-Rodríguez, R., Sangabriel-Conde, W., Mancera-López, M. E., Negrete-Yankelevich, S., & Barois, I. (2013). Loss of arbuscular mycorrhizal fungal diversity in trap cultures during long-term subculturing. *IMA Fungus*, 4(2), 161–167. <https://doi.org/10.5598/ima fungus.2013.04.02.01>
- Werner, G. D. A., & Kiers, E. T. (2015). Order of arrival structures arbuscular mycorrhizal colonization of plants. *New Phytologist*, 205(4), 1515–1524. <https://doi.org/10.1111/nph.13092>
- Wu, Q. S., Zou, Y. N., & He, X. H. (2010). Contributions of arbuscular mycorrhizal fungi to growth, photosynthesis, root morphology and ionic balance of citrus seedlings under salt stress. *Acta Physiologiae Plantarum*, 32(2), 297–304. <https://doi.org/10.1007/s11738-009-0407-z>
- Wubs, E. R. J., Van Der Putten, W. H., Bosch, M., & Bezemer, T. M. (2016). Soil inoculation steers restoration of terrestrial ecosystems. *Nature Plants*, 2(8), 1–5. <https://doi.org/10.1038/NPLANTS.2016.107>
- Wubs, E. R. J., van Heusden, T., Melchers, P. D., & Bezemer, T. M. (2019). Soil inoculation steers plant-soil feedback, suppressing ruderal plant species. *Frontiers in Ecology and Evolution*, 7(451), 1–8. <https://doi.org/10.3389/fevo.2019.00451>
- Zanchi, C. S., Batista, É. R., Silva, A. O., Barbosa, M. V., Pinto, F. A., dos Santos, J. V., & Carneiro, M. A. C. (2021). Recovering soils affected by iron mining tailing using herbaceous species with mycorrhizal inoculation. *Water, Air, and Soil Pollution*, 232(110), 1–13. <https://doi.org/10.1007/s11270-021-05061-y>
- Zhang, J., Wang, P., Xue, K., Hao, Y., Wang, Y., & Cui, X. (2019). Trait complementarity between fine roots of *Stipa purpurea* and their associated arbuscular mycorrhizal fungi along a precipitation gradient in Tibetan alpine steppe. *Journal of Mountain Science*, 16(3), 542–547. <https://doi.org/10.1007/s11629-018-5311-9>

SUPPORTING INFORMATION

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