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ABUNDANCE OF ARBUSCULAR MYCORRHIZAL FUNGI IN ORGANIC FARMLAND, CONVENTIONAL FARMLAND AND SECONDARY FOREST

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ABSTRACT

Understanding the effects of different agricultural practices on arbuscular mycorrhizal fungi (AMF) communities is important for sustainable agricultural production, since AMF play an essential role in maintaining and promoting the health of crop-plant communities. Previous studies have demonstrated that organic farming methods promote greater diversity of AMF in crops like cereal and maize, and have begun to investigate the relationship between compost and AMF in coffee crops. However, research on AMF abundance in agricultural systems in the tropics is generally lacking, especially with respect to the impact on AMF abundance of conventional farming methods – that use synthetic agrochemicals, like pesticides and fertilizers – and of organic farming methods – that do not use synthetic agrochemicals, but may use organic pesticides and fertilizers. My study investigated the AMF abundance in an organic versus a conventional coffee plot in a tropical cloud forest area in Costa Rica and compared these results to AMF abundance in a secondary forest (regrown after complete or partial clearance due to human activities) as a natural system. Soil samples containing roots collected from each site were analyzed microscopically, and mean AMF root percent colonization (proportion of each root that appeared to contain AMF) was determined for each site. AMF abundance was significantly greater in the secondary forest and the organic coffee plot when compared to the conventional coffee plot. AMF abundance did not differ significantly between the secondary forest and the organic coffee plot. These results show that different agricultural practices impact AMF communities, and highlight that organic farming supports an abundance of AMF similar to that found in natural ecosystems. In particular, my study demonstrates the ability of organic
farming to sustain more AMF compared to conventional farming, and the potential benefits of this increased abundance for sustainable agriculture.

INTRODUCTION

The global human population is expected to reach 9.8 billion by 2050, and grow to 11.2 billion by 2100 (United Nations 2017). Global food demand is rapidly increasing as a result (Tilman et al. 2011). However, under modern agricultural practices, consumption of agricultural products is responsible for simplification (loss of niche diversity) and destabilization of ecosystems (Ehrlich and Holdren 1971). This scenario creates a pressing need for intensification of agriculture to provide for our growing global population, while doing so in a sustainable manner that mitigates negative impacts of agricultural production and preserves ecosystem services such as air, water and soil. Suitable approaches include agroecosystems, which are mostly self-sustaining agricultural systems based on ecological principles (du Jardin 2015; Rains et al. 2011). Microbial parameters are effective indicators of soil quality changes and ecosystem health caused by land management (Bending et al. 2004). Such parameters may be used to assess replacement of conventional agricultural approaches based on synthetic agrochemicals and land conversion to increase food production (Lupatini et al. 2017) with agroecosystem-based approaches such as organic farming.

Arbuscular mycorrhizal fungi (AMF), a form of endomycorrhizal fungi belonging to the phylum Glomeromycota (Bonfante et al. 2010), may play an increasingly important role in sustainable agriculture and warrant further study. While more information about the effects of agricultural management on the microbial community is still needed (Li et al. 2012), the following background section describes what is currently understood about this interaction.
**Research question/hypothesis:**

This study seeks to understand how AMF abundance may differ among a secondary forest, a conventional monocultural coffee plot, and an organic monocultural coffee plot in a tropical cloud forest area. AMF abundance is measured via percent root colonization, frequently used to assess mycorrhizal colonization (Mahdhi et al. 2017), and abundance is discussed in the context of agroecosystem health.

**BACKGROUND**

The microbial community in the rhizosphere, a relatively shallow soil zone surrounding plant roots and influenced by both biotic and abiotic factors, can significantly impact the growth and health of plants in agroecosystems (McNear 2013; Philippot et al. 2013). Soil microbes comprise the majority of biodiversity in these soil ecosystems and are crucial for nutrient cycling (Pan et al. 2014; Navarrete et al. 2015) and plant health (Mazzola 2004; Wakelin et al. 2013).

**Symbiosis with arbuscular mycorrhizal fungi**

AMF specifically are obligate biotrophs, i.e., they colonize roots of a host plant and live on carbohydrates provided by the host plant (Bonfante et al. 2010). AMF have symbiotic associations with over 80 percent of terrestrial plant species (Harrier and Watson 2004). Upon colonization, nutrient exchange between plant and AMF occurs via AMF arbuscules, repeating branches of intracellular hyphae (fungal filaments) inside cells of the root cortex (the root’s outermost layer) (Bonfante et al. 2010). In this mutualistic interaction between AMF and plant, fungi take up carbohydrates in the form of hexoses (simple sugars with 6 carbon atoms per
molecule, like glucose and fructose) produced in photosynthesis by the plant, and the host plant conversely benefits as the AMF hyphal network increases root surface area by several centimeters for enhanced nitrogen and phosphorus acquisition, and provides defense against pests and pathogens (Bonfante et al. 2010; Kaiser et al. 2014; Philippot et al. 2013; Smith and Read 2008).

**Impacts of arbuscular mycorrhizal fungi on host plants**

The establishment of a hyphal network enables plants to communicate with each other about herbivory attacks and thus preemptively prepare defenses against pests (Philippot et al. 2013). AMF also contribute to the formation of a disease-suppressive soil, in which microorganisms inhibit formation or survival of pathogens through competition for microsites and nutrients. Other mechanisms of action by AMF include parasitism and amensalism, inhibition of one organism by another that remains unaffected, such as secretion of antimicrobial AMF metabolites that inhibit pathogen activity (Philippot et al. 2013). Because of these benefits, AMF are considered a biostimulant, a substance or microorganism that is applied to plants to enhance nutrient-acquisition efficiency, abiotic stress tolerance, and/or crop quality traits (du Jardin 2015). AMF have “high-affinity inorganic phosphate transporters” that serve to significantly improve soil nutrient provision to the host plant (Bonfante et al. 2010). In addition, AMF aid in translocating nutrients from surrounding bulk soil (without plant roots) to the depletion zone of the plant rhizosphere (zone around the root system and fungal hyphae), where the concentration of nutrients is lower than in bulk soil due to continuous uptake by roots and hyphae (Gosling et al. 2006; Schneider et al. 2015). AMF also increase plant resilience to both biotic stressors (e.g., pests and pathogens) and abiotic stressors (e.g., drought, heat, or nutrient deficiency), improve
host water balance, and affect plant development by modulation of the levels of plant hormones (phytohormones) that regulate plant development, stress response, and formation and operation of the AMF symbiosis with its effects on root architecture, growth, and flowering (Augé 2001; Gosling et al. 2006; Gianinazzi et al. 2010; Harrier and Watson 2004; Pozo et al. 2015). The latter changes caused by AMF may contribute to root system remodeling (Gutjahr and Paszkowski 2013). Finally, AMF act via physical mechanisms that stabilize soil, such as the formation of a microporous soil structure with large particle size that enhances flow of air and water and prevents erosion (Oehl et al. 2003).

**Impact of arbuscular mycorrhizal fungi on photosynthesis**

AMF influence the source-sink balance in plants and promote photosynthetic upregulation (Adams et al. 2018). Photosynthesis is the source of sugars, while the sugar-consuming non-photosynthetic parts of the plant (e.g., stems, roots, flowers, fruits) are the plant’s sinks for sugars (Adams et al. 2018). However, additional sinks for sugar can also occur beyond the plant’s own tissues. AMF, along with other symbiotic soil microbes, consume sugars and thus increase sink activity; in response, the plant increases its photosynthetic capacity to meet this increased demand for sugars (Adams et al. 2018). Conversely, downregulation of photosynthesis by reduced sink activity was demonstrated in an experimental setting, where seedling of the host plant *Pinus strobus* underwent a quick decline in photosynthetic rate when significant portions of the mycorrhizal sink were removed (Lamhamedi et al. 1994). Abiotic factors can affect the impact of mycorrhizae on photosynthetic activity; falling temperatures may eliminate photosynthetic upregulation in response to microbes, likely because the cold slows down fungal and plant growth (Shrestha et al. 1995). On the other hand, many studies have demonstrated that
mycorrhizae can ameliorate adverse impacts of various abiotic factors, including limited nutrient and water availability, heat stress, salinity, low temperature, and compacted soil (Adams et al. 2018).

**Minimal role of arbuscular mycorrhizal fungi in conventional agriculture**

The efficiency of plant root systems, and sometimes the degree of colonization by AMF, of landraces (domesticated, locally adapted, and traditional crop species) are greater than those of high-yielding elite agricultural crop lines used in conventional systems (Newton et al. 2010). While conventional plant breeding and agricultural production has been successful under high inputs of water, nutrients, and pesticides, productivity of conventional systems decline sharply in low-input environments like organic farming systems, in which landraces with more extensive root systems and symbiotic microbes may perform better (Newton et al. 2010). The high level of inputs in conventional systems may have inadvertently decreased the ability of elite crops to host AMF and reap the benefits of the symbiotic relationship, including water and nutrient acquisition and defense against insects and disease (Newton et al. 2010). For this reason, rhizosphere microbiota are often found to be comparably less important in conventional agricultural systems with high input of fertilizers and pesticides, low biodiversity, and minimal interaction between microbiota and plants (Philippot et al. 2013). It will be essential to investigate the role microbiota can play in sustainable agricultural approaches that draw upon natural sources of increased nutrient availability and pathogen control (van Bueren et al. 2002).
Role of arbuscular mycorrhizal fungi in organic agriculture

An understanding of AMF is clearly important as their symbiosis with plants provides ecosystem services that promote crop productivity and quality in sustainable agricultural systems (Gianinazzi et al. 2010), and the sustainability of agroecosystems can likely be improved by maintaining a healthy population of beneficial microorganisms like AMF (Lupatini et al. 2017). Transitioning to organic farming approaches that utilize microbiota such as AMF may also make contributions to lessening the current loss of biodiversity, while increasing sustainable food production (Gonthier et al. 2014). Consequently, an understanding of how different agricultural practices affect this mycorrhizal symbiosis is necessary for the design of optimal management strategies for sustainable agroecosystems (Turrini et al. 2017; Harrier and Watson 2004; Manoharan et al. 2017). This understanding is especially important since relatively little attention has been paid to the role of beneficial soil microorganisms (including AMF) in agriculture since the first green revolution (Gianinazzi et al. 2010).

Recent studies, conducted in various geographic locations and agricultural systems, have analyzed different indicators of AMF health in relation to agricultural management methods. In east China, addition of organic compost to a subtropical wheat-rice rotation agroecosystem significantly enhanced hyphal and spore biomass of AMF (Qin et al. 2015). In southern Sweden, organically farmed cereal fields exhibited greater AMF diversity than their conventionally farmed counterparts (Manoharan et al. 2017). In the latter study, high AMF diversity was positively related to phosphorus uptake by barley and to grain biomass production (Manoharan et al. 2017).

Several studies conducted in the tropics have illustrated that *Coffee arabica* benefits from inoculation with AMF and treatment with organic compost (Rojas et al. 2019; Osorio et al. 2002;
Rivera et al. 2007). However, investigation of the qualities of AMF under organic versus conventional management in the tropics is generally lacking, despite the possibility that native fungal strains may play an even more crucial role as biofertilizers in the processes of phosphorous transformation and absorption in coffee plants in tropical soils (Rojas et al. 2019), since highly weathered tropical soils are low in both total and biologically available phosphorus (Friesen et al. 1997).

MATERIALS AND METHODS

Study Site
Both coffee plots and the secondary forest were located at Life Monteverde, a 17-hectare farm in Monteverde, Costa Rica, in the premontane wet forest. The organic and conventional plots were adjacent to each other, separated by a trail and two live fences. Both plots were planted 7 years ago, both were coffee monocultures, and both were sun plantations of approximately 0.2 hectares. Both plots were managed identically excepting fertilizer use. The conventional plot (Fig. 3), received three rounds of chemical fertilizer and was treated with about 184 kg of fertilizer per year, consisting of both a nitrogen formula and a complete formula (blend of nitrogen, phosphorus, and potassium). The organic plot was treated with 6,810 kg of organic compost (or about 6 kg of compost per coffee plant) per year, created at the farm using livestock feces and organic waste. The patch of forest was completely removed from both plots, on the periphery of the farm.
Sample Collection

Samples were collected from the organic plot on 29 October 2018, and from the conventional plot and forest on 7 November 2018. Using a 50-cm-long soil core sampler, 10 topsoil samples were collected at each site (for a total of 30 samples), up to a depth of 10 cm. Cores were extracted 10 cm from the base of plant individuals, and each individual was approximately the same size (about 20 cm in diameter at knee height). Upon extraction, soil cores were placed into individual ziploc bags and sealed. Samples were collected at least one meter apart from each other within each site. Moreover, samples were not collected from adjacent individuals in the plots nor in the forest. In the forest, five samples were taken on each side of a man-made trail which divided the forest fragment into two sides. These samples were collected at least three meters into the forest, away from the trail. Within each plot, two soil samples were taken at each of five locations (the edge of each plot in each cardinal direction comprising four of the locations, and the approximate center of the plot comprising the fifth), to better encompass potential variation within a plot.

All coffee plants were of the same species, but other, interspersed plant individuals in the forest were of different, unidentified species. Samples from the organic plot were stored in the refrigerator in their original ziploc bags for approximately 3 days before being cleaned and processed, whereas samples from the conventional plot and forest were cleaned and processed on the same day they were collected. Refrigeration of roots in their original soil samples does not adversely impact AMF biomass (Dr. Karen Masters, personal communication).
AMF Staining

Out of the 10 samples from each site, 5 were randomly chosen for processing and analysis. Soil from each chosen sample was passed through a 2-mm soil sieve (Fig. 1), and each extracted root was rinsed with tap water and gently scrubbed by hand to remove soil particles. Roots were handled very carefully to avoid disturbing the outer root layer where AMF arbuscules reside (Bonfante et al. 2010). Four roots were chosen from each of the 5 samples, for a total of 20 roots per site, resulting in 60 total roots from the 3 sites. Roots were preferentially selected if they were at least 10 mm in length, were thin, and were pale or lacked pigment (to make microscopic analysis easier). Then roots were cleared using a modified version of the Phillips and Hayman (1970) method altered as described by Koske and Gemma (1989). Clean roots from a specific site were immersed in a glass beaker of approximately 100 ml of 3% KOH solution at 90°C for 90 minutes. Then roots were removed from the bath using forceps, and placed in clean plastic Petri dishes. Next, alkaline H$_2$O$_2$ was pipetted over the roots until all roots were completely covered in solution (Fig. 2). A lid was placed on the Petri dish(es) and the roots were then soaked for 30 minutes at room temperature to complete the clearing process. Then, roots were removed and placed in clean Petri dishes again using forceps for transfer, and were completely covered by a solution of 1% HCl (administered using the same technique) and left to soak at room temperature for one hour while covered. Finally, roots were transferred to clean Petri dishes, where they were submersed in a room-temperature solution of acidic glycerol with approximately 5 ml of 0.05% trypan blue dye. Trypan dye was stored in a cool, dark place between uses. After covering the Petri dishes, roots were left to soak overnight for 18 hours to complete the AMF staining process. After 18 hours, roots were again moved to clean Petri dishes prior to quantification of AMF colonization.
Figure 1. Roots from a soil sample after sieving and prior to gentle scrubbing to remove remaining soil particles. Roots were selected that were similar in pigmentation and morphology to those pictured – pale or translucent, and thin.
Figure 2. Image of roots soaking in alkaline H₂O₂ during chemical processing. Samples were cleaned and placed in Petri dishes following processing.

Quantification of AMF abundance

Each root was placed on a microscope slide after processing, and observed using a compound microscope under 100x magnification. After scanning the entire root, the segment that appeared most densely colonized by AMF, which looked like blue vesicles and/or hyphal branches (Fig. 4), was photographed using a microscope digital camera adaptor. Once photos were taken using the same methodology for all 60 roots, the photos were exported to Microsoft PowerPoint, where each was sized to 28.63 cm wide and 19.05 cm tall. A transparent 8x8 grid (22.67 cm wide and 8.23 cm tall, with individual cells of 2.84 cm width and 1.14 cm height), created using the table function of PowerPoint, was placed horizontally on each photo (Fig. 5). The rectangular grid was
aligned with the longest side parallel to the longest side of the photo, within the root area (no part of the grid extended into any blank space in the background of the photo). The grid was placed over the portion of the photographed root that appeared to be most populated by AMF. Then, the number of grid squares (out of 64) in which there were any blue AMF hyphae or spores were counted as “present.” The number of present squares were totaled for a root and then divided by 64 (total number of grid squares) to calculate percent colonization by AMF. This quantification process was repeated for all 60 roots.

**Statistical analysis**

Since percent colonization data were not normally distributed, the differences in median AMF percent colonization of roots between secondary forest, organic coffee plot, and conventional coffee plot was assessed via non-parametric analysis by the Kruskal-Wallis test, then using post-hoc pairwise comparisons between means according to Mann-Whitney U tests following the detection of significant differences between treatments using a Kruskal-Wallis test. The Holm’s method was used to correct for multiple comparisons.
RESULTS

The coffee plants in the conventional plot and the organic plot appeared equally healthy as per visual appearance and Figure 4 shows examples of roots with AMF colonization from the three sites. Sites differed in root AMF percent colonization (Kruskal-Wallis 18.375, df = 2, p = 0.0001). AMF percent colonization per root was significantly lower in the conventional plot than in either the organic plot or the forest, with the latter two sites not differing from each other (Fig. 6).

Figure 3. Photograph taken from atop a hill, overlooking the conventional coffee plot in Life Monteverde. Coffee plants were visually assessed to be of similar height, about 175 cm, and thus of similar age. The plot was surrounded by live fences (a single row of trees, on each side of the plot, that separate this plot from other plots). More plots and forest fragments made up the rest of the area. The organic coffee plot, on the other side of one of the live fences (but not pictured) was visually indistinguishable. Soil samples were collected from both coffee plots.
Figure 4. Photographic images of arbuscular mycorrhizal fungi (AMF) in plant roots, taken at 100x magnification under a compound microscope. AMF may exist as hyphae, arbuscules, and/or vesicles. From left to right: a root from an organic coffee plot, a root from a conventional coffee plot, and a root from a nearby secondary forest. These photographs are not necessarily representative of mean AMF percent colonization for each of these 3 sites, but provide examples of how AMF appear under the microscope after processing, and show the types of photos used during percent quantification.

Figure 5. Photograph of root from the organic coffee plot with grid overlay for analysis of AMF colonization. After export to Microsoft PowerPoint, each photo was sized to 28.63 cm wide and
19.05 cm tall. The grid was horizontally aligned with the most densely colonized area of the root segment, as determined by appearance, for each photo. The quantity of grid squares with AMF ‘present’ (any amount of blue fungi within the square(s)), was divided by the total quantity of grid squares (64) to determine percent colonization by AMF.

Figure 6. Percent cover with arbuscular mycorrhizal fungi (AMF) on roots of coffee plants from a conventional coffee plot, a nearby secondary forest in premontane wet forest, and an organic coffee plot in Monteverde, Costa Rica. Boxes show the 25\textsuperscript{th} and 75\textsuperscript{th} percentile of the data, with
DISCUSSION

While AMF were present in all three sites, the conventionally managed plot had a significantly lower density of AMF colonization than the other two sites. In addition, secondary forest and the organic plot supported similar abundances of AMF. These results provide insight into how different agricultural management practices, specifically of a valuable tropical crop like coffee, affect AMF abundance. These results also demonstrate that agricultural practices can alter AMF abundance from a relatively undisturbed state in a secondary forest in the Costa Rican premontane wet forest.

The absence of a significant difference in AMF abundance between the organic coffee plot and secondary forest indicates that the organic crop supports AMF communities at a similar level as the forest. This finding is consistent with a previous report that tropical coffee production systems exhibit similar diversity of AMF species as a tropical montane cloud forest patch in Mexico, as measured by AMF spore diversity in topsoil (Arias et al. 2012). My study was conducted on a similar agricultural site in a very similar ecosystem with respect to altitude and climate, but differs from the study by Arias et al. (2012) in that I analyzed AMF abundance via root colonization as opposed to AMF diversity through morphospecies identification of
spores, in which AMF taxonomic species were distinguished solely by morphological differences between spores. Furthermore, my study examined the abundance of AMF in coffee production in a geographic region in which this topic had not been previously investigated. Studying AMF abundance is particularly valuable since reduction in abundance of microbial parameters (AMF included) is a consistent indicator of management-induced changes to soil quality (Bending et al. 2004). Higher AMF abundance may indicate that use of compost in tropical agriculture promotes healthier soils.

The reduced AMF abundance in the conventional plot highlights the negative impact of conventional agricultural practices on the prevalence of beneficial AMF communities in tropical cropland, which could have critical implications for crop health (Gosling et al. 2006). While more work is needed to design management practices that support microbial community health, it has been repeatedly shown that microbial diversity increases under organic management compared to conventional management (Mader et al. 2002; Hartmann et al. 2015). The symbiosis between crop plants and AMF generally increases plant performance in soils of low nutrient status, as AMF provide plants with nutrients, particularly less mobile ones like phosphorus (Thingstrup et al. 1998). Thus, abundant and diverse AMF communities may be required for maintenance of desirable yields of many crop species in low-P soils (Barea and Jeffries 1995; Bethlenfalvy and Linderman 1992; Miller et al. 1995). A positive response by coffee plants to AMF inoculation has been documented under tropical soil conditions (Rivera et al. 2007). Osorio et al. (2002) found improved growth of *C. arabica* seedlings in response to organic approaches and AMF inoculation, in comparison to coffee plants in unamended soil. Furthermore, mycorrhizal coffee plants exhibited better growth than non-mycorrhizal plants, which was associated with higher accumulations of N, Ca and Mg (Vaast and Zasoski 1992).
The fact that both conventional and organic plots appeared equally healthy (similar in plant height and density, etc.) in my study suggests that the reduced abundance of AMF in the conventional plot might have been be compensated for by application of agrochemicals such as synthetic fertilizers. Conversely, the higher density of AMF colonization in the organic versus the conventional plot is likely due to the exclusion of fertilizers, fungicides, and many biocides (Gosling et al. 2006; Thingstrup et al. 1998). The decrease of microbial diversity and abundance under conventional agricultural practices is presumably due to direct or indirect stresses caused by agrochemicals, which may inhibit or exterminate some species of microbes and allow only a limited group of other microbes to thrive (El Fantroussi et al. 1999; Liu et al. 2007; Stagnari et al. 2014; Lupatini et al. 2017). Additionally, the use of compost itself in the organic plot, rather than solely the absence of agrochemicals, may be responsible for higher AMF abundance in the organic plot.

Rhizosphere microbiota encourage resilient agricultural systems by enabling enhanced resistance to and recovery from pests and pathogens (Philippot et al. 2013). Compost and livestock manure support these biological practices by providing rich substrate in the soil that generates diverse habitat niches for a greater variety of microbes, thereby increasing community diversity (Lupatini et al. 2017). While AMF inoculation and compost application each independently increased the yield and nutrient uptake of wheat in a laboratory experiment in Pakistan, the greatest improvement was observed as a result of the combination of inoculation with AMF and addition of compost (Jan et al. 2014). Such a synergistic effect may also be at play in coffee crops, given that compost-treated coffee supported higher AMF abundance in a tropical cloud forest area.
RECOMMENDATIONS FOR FUTURE RESEARCH AND MANAGEMENT IN THE CONTEXT OF CLIMATE CHANGE

Further studies should be conducted to assess the specific relationship between compost and AMF communities, and to provide insight into how the combination of AMF and compost may best be exploited to improve crop yield.

Currently, organic agriculture in developing countries like Costa Rica produces an average of 43% less yield than conventional agriculture in these same areas (Seufert 2012). While this difference may be due to a multitude of abiotic and biotic factors, the demonstrated positive impact of AMF on organic crops in terms of enhanced yield, pest and disease resistance, stress tolerance, and nutrient acquisition presents a promising outlook for the future of organic agricultural production in developing nations with tropical ecosystems. In Sweden, Manoharan et al. (2017) increased barley and ley grassland biomass output in organic agricultural approaches by promoting AMF abundance and diversity, which positively impacted root biomass and phosphorus uptake. The latter authors proposed that higher AMF diversity is linked to the practices of organic farming, particularly the administration of manure to crops, and that enhanced AMF presence improves soil P acquisition. Although the study conducted by Manoharan et al. (2017) was not in a tropical ecosystem nor in a developing nation, the finding is likely applicable to the agricultural settings found in Costa Rica. Similarly, AMF are biofertilizers (that enhance growth by increasing nutrient supply to the host), i.e., the fungi support nutrient-use efficiency of available nutrients by plants as assessed via biomass yield per unit nutrient input (Rouphael 2015). Therefore, AMF use in organic farming, particularly in a phosphorus-deficient tropical cloud forest ecosystem, may be able to substitute for reduced fertilizer and biocide inputs (Gosling et al. 2006; Andrade et al. 2009). It is possible that AMF
could compete with plants for nitrogen, since nitrogen concentration is higher in AMF biomass than in plant biomass, but the frequency and extent of competition between AMF and crops for nitrogen is undetermined in agroecosystems (Wang et al. 2018). Together, these findings support the notion that Costa Rican agriculture could benefit from higher AMF abundance and phylogenetic diversity, as induced by organic farming techniques, which may reduce reliance on agrochemicals and enhance ecosystem services and crop yields (Andrade et al. 2009).

Soil acts as a pool for the majority of terrestrial carbon (Jobbágy and Jackson 2000), and since the industrial revolution began, 136+/−55 billion tons of carbon have been emitted due to land use change and soil cultivation alone (Lal 2004). Particularly in the context of current global climate change, and the resulting positive feedback loop between warming and soil carbon stock decomposition (Davidson and Janssens 2006), it is imperative to understand how shifts in atmospheric and soil gas composition affect soil and crop health (Jobbágy and Jackson 2000), as well as the role of the rhizosphere community in maintaining soil structure, crop integrity, and terrestrial carbon storage. This insight will be critical to transition to sustainable agriculture that both adapts to, and mitigates, unprecedented environmental transformation. Climate change is expected to directly affect microbial ecology since increasing CO2 will likely change soil food web interactions and plant root exudation (Philippot et al. 2013). In turn, the microbial community itself is also expected to influence greenhouse gas levels and buffer agroecosystems from potential climate change-induced events. AMF facilitate the sequestration of carbon in the soil (Philippot et al. 2013), an increasingly important activity as atmospheric carbon dioxide levels rise. Soil microorganisms are more adaptable than their hosts, and the vast diversity of microorganisms increases the odds that there are microorganism taxa well-adapted to warmer conditions (Philippot et al. 2013). Broad geographic range of soil microbiota may also facilitate
migration of plant species to more suitable microclimates as temperatures increase, and the 
spread of soil-borne fungi may shift soil food webs to those dominated by fungus, which changes 
agroecosystem response to drought and other extreme weather events exacerbated by climate 
change (Philippot et al. 2013).
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