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Richness and abundance of filamentous fungi in complex agroforestry multistrata system soil

Riquesa e abundância de fungos filamentosos em solo de sistema agroflorestal multiestrato

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ABSTRACT: Fungi are important components of soil microbiota as they are vital to the maintenance and functioning of agroforestry systems soils. This is due to their involvement in key processes such as the cycling of organic matter, besides establishing different ecological interactions with other organisms. In this study, the diversity, species richness and composition of the community of the soil filamentous fungi were investigated during two years. One hundred and ten species were identified consisting mostly of saprobes. Some species are also potential antagonists of plant pathogens. Diversity of soil filamentous fungi and its richness were high. This fungi community has few dominant species and many rare species with niche overlapping patterns and an intermediate uniformity. The structure and management of the agroforestry system provide a diversity of plant residues with different chemical characteristics that will determine a greater diversity of niches for the filamentous fungi community.

KEYWORDS: Fungal diversity; Mycobiota; Community structure.

RESUMO: Os fungos são componentes importantes da microbiota do solo, pois são vitais para a manutenção e o funcionamento dos solos dos sistemas agroflorestais. Isto é devido ao seu envolvimento em processos chaves, como o ciclo da matéria orgânica no sistema, além de estabelecerem diferentes interações ecológicas com outros organismos. Neste estudo, a diversidade, riqueza de espécies e composição da comunidade dos fungos filamentosos do solo foram estudadas durante dois anos. Foram identificadas 110 espécies, no qual a maioria é considerada sapróbia. Algumas espécies também são potenciais antagonistas de patógenos de plantas. O sistema apresentou alta diversidade de fungos filamentosos no solo. A comunidade de fungos é composta por poucas espécies dominantes e muitas espécies raras com padrões de sobreposição de nicho. A estrutura e manejo do sistema agroflorestal disponibilizam uma diversidade de resíduos de plantas com diferentes características químicas que determinam uma maior diversidade de nichos para a comunidade de fungos filamentosos.

PALAVRAS-CHAVE: Diversidade de fungos; Micobiota; Estrutura da comunidade.

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Introduction

Agroforestry systems have already proven to be a viable and sustainable alternative to agricultural practices as they minimize the effects of human activities. The purpose of that system of land use is to take advantage of the increased biodiversity as a factor of dynamic equilibrium as seen in complex ecosystems like natural forests. The success of crops in high plant species diversity has shown that biodiversity can be an important tool for the balance in the interaction between plants, animals and microorganisms (JOSE, 2012).

Agroforestry has the potential to conserve soil and maintain its fertility and productivity. The canopy formed by the diversity of taller plants provides ground cover due to the deposition of a dense layer of dead organic matter continuously produced by the falling leaves and branches of different cultivated plants (JOSE, 2009). This increases the protection against soil erosion, reduces rainwater runoff by enhancing its infiltration, and consequently helps to reduce soil nutrients leaching. The litter layer reduces soil temperature and increases the amount of organic matter, therefore, soil chemical, physical and biological properties are improved (ARAUJO et al., 2012; FIALHO et al., 2013).

Among the microorganisms found in soil, the fungi stand out. Their main role is the heterotrophic activity on organic matter. Fungi are important components of soil microbiota (BOER et al., 2005). The organization and functioning of fungal communities govern biochemical changes in the soil and are central to the maintenance and operation of natural and agricultural soils due to their involvement in key processes such as soil structuring, organic matter cycling, and humus formation, which can contribute to changing the availability of nutrients and toxic elements in the soil, but also to change the chemical properties of the soil (GOMES et al., 2003; GARBEVA et al., 2004).

The study of the mycobiota composition is particularly important for cultivated soils as these consist of heavily modified habitats. The importance of fungal community structure rests both in the possibility of predicting changes in the functioning of agricultural systems as a result of changes in fungal composition, and in the potential development of sustainable agricultural systems that conserve soil mycobiota, such as the agroforestry systems (BRESOLIN et al., 2010; COSTA et al., 2012; ARIAS and ABARCA, 2014). The knowledge about the soil mycobiota can contribute to the knowledge of fungal taxonomic diversity and possible roles these populations may be playing in the system. The aim of this work was to study the composition of the soil mycobiota (fungal community structure) in an agroforestry system.

Materials and Methods

Study area

This research was carried out in the Sítio São João (7°53'13"S and 34°53'43"W), located in the municipality of Abreu e Lima, in the metropolitan region of Recife, Pernambuco, Brazil. The vegetation physiognomy in this region corresponds to Dense Ombrophilous Atlantic Forest. The annual average rainfall in the region is approximately 1,700 mm with two well-defined seasons: rainy from April to September and dry from October to March (APAC, 2016). Soils are predominantly oxisols (Ustox) of the sandy loam textural class.

Currently, this agroforestry is classified as a complex multistrata agroforestry system (CMAFS) (SCHROTH and SOCORRO, 2014). It has three strata that are composed of native and exotic trees, some bearing fruits of economic interest (COSTA et al., 2016). Handling of the agroforestry system is carried out through pruning, and the plant residues from the harvest of short-cycle species or pruning of long cycle species, besides the naturally fallen material are left on the soil surface to form a thick litter layer. Pesticides and chemical fertilizers are banned, and nitrogen is supplied by fertilizing plants (*Clitoria racemosa* Benth. and *Canavalia ensiformis* DC.).

Soil samplings

Eight quarterly collections of soil were carried out during two years of sampling, in which the first year corresponds to the period from August 2011 to July 2012 and the second year from August 2012 to July 2013. In the studied area, 10 random sampling points (repetitions within the area) were marked observing a distance of at least 10 meters from one point to another. In each sampling point, three simple equidistant (0.5 m) soil samples were collected to a depth of 0-15 cm, which were homogenized in equal volumes to produce one composite soil sample.

Isolation and identification of filamentous fungi

Fungi were isolated using the serial dilution method, in which 25 g of soil were added to 225 ml of sterile distilled water. Subsequently, serial dilutions were made up to 10-3. In which, 1 mL of the last dilution was removed and inoculated onto Sabouraud Agar (SA, g / L distilled water: 40 dextrose, 10 peptone, 15 agar), pH was adjusted at 5.5, and chloramphenicol (100mg / ml)

and Rose Bengal (0.05g / L) were added. The experiment was performed in triplicate. The plates were incubated at 27ºC ± 2ºC in laboratory conditions for 10 days. After the growth of colonies, the density of fungi was determined by direct plate counting and the results expressed as Colony Forming Units per gram of soil (CFU / g of soil). The average of CFU of the triplicate plates was calculated to give CFU per sampling point. These results were submitted to the analysis of variance and, when significant, paired comparisons of averages were calculated using the test of Tukey at 5% probability. Pearson correlation was calculated between the fungal density and monthly rainfall. The precipitation values for Abreu e Lima municipality were obtained from the Pernambuco Water and Climate Agency (APAC, 2016).

The colonies developed in the CFU plates were sub-cultured to SA plus chloramphenicol (100 mg/ml) until single axenic colonies were obtained. In the process of identification, macroscopic (color, appearance and diameter of colonies) and microscopic (somatic and reproductive microstructures) characteristics were observed. The fungi were identified with the help of URM Culture Collection personnel at the Mycology Department, at the Universidade Federal de Pernambuco, Brazil.

Diversity analysis

Univariate community indices: after the identification of the filamentous fungal species from the different soil samples, the following univariate indices were applied: Species Richness; Shannon-Wiener's Diversity (H'); Pielou's Equitability (J'); Berger-Parker's Dominance (d). The univariate indices were calculated using the program PAST 2.17c (HAMMER et al., 2013) for each year of research and applied bootstrap (1000 random sample), generating 95% confidence intervals for the values found.

Richness Estimation: to estimate the filamentous fungi species richness in the agroforestry soil, the estimators Jackknife 1 (SJack1) and Jackknife 2nd Order (SJack2) were applied. The estimators were calculated using the software EstimateS 9.10 (COLWELL, 2013), as well as the associate confidence intervals of 95%.

Results and Discussions

Mycobiota composition in the agroforestry system soil

Fungi density for the first and second year was respectively 1,801 x 103 and 1,761 x 103 CFU g soil -1, showing no significant difference (p = 0,78). Fungal density showed a strong positive correlation (r = 0.88; n = 8; p = 0.0042) with rainfall, suggesting that increased rainfall causes an increase in the density of fungi in soils. The density increasing was probably related to moisture, as suggested by Souto et al. (2008), who found changes in fungal densities according to soil moisture levels.

In this work, 110 fungal species distributed in 45 genera have been identified. The species belong to the phyla Ascomycota, Basidiomycota, and subphylum Mucoromycotina. The most representative genera were *Penicillium*, (38 species) *Aspergillus* (16 species), and *Trichoderma* (7 species). These genera of fungi are often reported in soil ecosystems (CAVALCANTI et al., 2006; SCHOENLEIN-CRUSIUS et al., 2006; ARIAS and ABARCA, 2014).

The high density of *Penicillium* can be directly related to the antagonism of these species relative to other by antibiosis, by producing secondary metabolites, or indirectly by nutritional competition, and higher production of spores (NICOLETTI and DE STEFANO, 2012). This genus may also contribute to soil fertility as species of *Penicillium* have great capacity of phosphate solubilization (PANDEY et al., 2008; DEEPA et al., 2010).

Species of *Penicillium* and *Aspergillus* are producers of many hydrolytic enzymes, which confer the ability to use different substrates in the soil, especially lignocellulosic materials. Therefore, they predominate over other fungal populations that use only specific substrates and/or labile substances (GOMEZ et al., 2007). In agroforestry, the presence of *Aspergillus* spp. and *Penicillium* spp. is common, with records of isolation from agroecological vineyards (RECH et al., 2013), integrated crops of blackberry, raspberry and blueberry (PINOTTI et al., 2011), and fruit trees of *Citrus* (PRADE et al., 2007) in southern Brazil, as well as agroforestry multistratified soil in the State of Pernambuco (COSTA et al., 2012).

Silva et al. (2011) isolated fungi from agroforestry soil in Bom Jardim-PE and rated the enzymatic production of these fungi. They found that species of *Penicillium* and *Aspergillus* were more efficient in the degradation of cellulose when compared to other species of fungi. Biodegradation of lignocellulosic materials is a major event in the carbon cycling process, due to the abundance of these materials in most terrestrial ecosystems.

Fungal species identified in this work (Table 1) are considered common soil inhabitants, however, the distribution of the fungal community in the ground is related to climate, vegetation and quality of soil organic

Table 1. Filamentous fungal species isolated from agroforestry soil. First year (August, 2011 to July, 2012) and second year (August, 2012 to July, 2013). Figures expressed in number x 103 Colony Forming Units g soil -1.

Species	First year	Second year
Absidia cylindrospora Hagem	0.01	0.00
Acremonium curvulum Gams	0.21	0.58
Acremonium recifei (Leão & Lôbo) Gams	0.32	1.68
Acremonium terricola Gams	0.13	0.05
Acrostalagmus luteoalbus (Link) Zare, Gams & Schroers	0.10	0.05
Aspergillus aculeatus Lizuka	1.48	0.70
Aspergillus deflectus Fennell & Raper	0.01	0.00
Aspergillus flavus Link	0.18	0.18
Aspergillus funiculosus G. Sm.	0.08	0.01
Aspergillus japonicus Saito	0.82	1.84
Aspergillus niger Tiegh	2.65	2.70
Aspergillus ochraceus Wilh.	0.10	0.04
Aspergillus parasiticus Speare	0.21	0.29
Aspergillus puniceus Kwon-Chung & Fennell	0.02	0.00
Aspergillus sclerotiorum Huber	0.02	0.00
Aspergillus sulphureus Desm.	0.02	0.00
Aspergillus tamarii Kita	0.25	0.00
Aspergillus terreus Thom	0.28	0.24
Aspergillus terricola Marchal & Marchal	0.05	0.00
Aspergillus unguis (Émile-Weill & Gaudin) Thom & Raper	0.01	0.00
Aspergillus ustus (Bainier) Thom & Church	0.02	0.00
Aureobasidium pullulans (de Bary & Löwenthal) Arnaud	0.04	0.00
Beauveria brongniartii (Sacc.) Petch	0.12	0.01
Cladosporium cladosporioides (Fresen.) Vries	0.20	0.33
Clonostachys candelabrum (Bonord.) Schroers	0.18	0.05
Clonostachys rosea (Preuss) Mussat	0.07	0.08
Cunninghamella elegans Lendn.	0.21	0.71
Curvularia lunata (Wakker) Boedijn	0.11	0.23
Curvularia pallescens Boedijn	0.00	0.36
Curvularia senegalensis (Speg.) Subram.	0.02	0.08
Eurotium repens Bary	0.01	0.00
Fusarium lateritium Nees	0.05	0.05
Fusarium nivale Ces. ex Berl. & Voglino	0.12	0.32
Fusarium oxysporum Schltdl.	036	0.27
Fusarium redolens Wollenw.	0.02	0.00
Fusarium solani (Mart.) Sacc.	0.36	0.21
Geotrichum candidum Link	0.02	0.00
Gliocladium virens J.H. Mill., Giddens & A.A. Foster	0.66	0.38
Gliomastix murorum (Corda) Hughes	0.22	0.13

Gongronella butleri (Lendn.) Peyronel & Dal Vesco	1.12	1.30
Gonytrichum macrocladum (Sacc.) Hughes	0.00	0.02
Humicola fuscoatra Traaen	0.30	0.27
Ilyonectria destructans (Zinssm.) Rossman, L. Lombard & Crous	0.04	0.06
Lecanicillium fungicola (Preuss) Zare & Gams	0.02	0.00
Metarhizium anisopliae Sorokīn	0.36	0.09
Myrothecium verrucaria (Alb. & Schwein.) Ditmar	0.06	0.11
Paecilomyces marquandii (Massee) Hughes	0.10	0.00
Penicillium aurantiogriseum Dierckx	1.39	2.33
Penicillium bilaiae Chalab.	0.09	0.00
Penicillium brevicompactum Dierckx	0.55	0.51
Penicillium canescens Sopp	0.01	0.00
Penicillium chrysogenum Thom	0.18	0.00
Penicillium citreonigrum Dierckx	0.48	0.62
Penicillium citrinum Thom	0.88	0.53
Penicillium commune Thom	0.51	0.00
Penicillium corylophilum Dierckx	0.08	0.36
Penicillium decumbens Thom	0.20	0.10
Penicillium dierckxii Biourge	0.00	0.03
Penicillium duclauxii Delacr.	0.00	0.14
Penicillium echinulatum (Dale)	0.02	0.00
Penicillium funiculosum Thom	0.00	0.02
Penicillium glabrum (Wehmer) Westling	0.44	0.30
Penicillium griseofulvum Dierckx	0.13	0.12
Penicillium implicatum Biourge	0.31	0.13
Penicillium islandicum Sopp	0.01	0.00
Penicillium janczewskii Zalessky	0.31	0.10
Penicillium janthinellum Biourge	1.03	0.53
Penicillium javanicum Beyma, Verh. Akad. Wet.	0.00	0.11
Penicillium melinii Thom	0.84	0.46
Penicillium miczynskii Zalessky	0.35	0.18
Penicillium minioluteum Dierckx	0.38	0.12
Penicillium parvum Raper & Fennell	0.00	0.12
Penicillium pinophilum Hedgc.	1.61	1.60
Penicillium purpurogenum Flerov	1.26	1.17
Penicillium restrictum Gilman & Abbott	0.69	0.18
Penicillium sclerotiorum Beyma	0.18	0.00
Penicillium simplicissimum (Oudem.) Thom	1.51	3.30
Penicillium solitum Westling	0.92	1.07
Penicillium thomii Maire	0.02	0.00

Penicillium turbatum Westling	0.80	0.51
Penicillium varians G. Sm.	0.00	0.01
Penicillium verruculosum Peyronel	3.76	3.50
Penicillium vinaceum Gilman & Abbott	0.00	0.05
Penicillium vulpinum (Cooke & Massee) Seifert & Samson	0.00	0.16
Penicillium waksmanii Zalessky	0.32	0.17
Pestalotiopsis maculans (Corda) Nag Raj	0.29	0.28
Phialophora cyclaminis Beyma	0.24	0.00
Phoma eupyrena Sacc.	0.00	0.04
Purpureocillium lilacinum (Thom) Hywel-Jones & Samson	3.19	3.16
Sarocladium strictum (Gams) Summerb.	0.28	0.17
Scedosporium apiospermum Sacc. ex Castell. & Chalm	0.18	0.49
Scopulariopsis asperula (Sacc.) Hughes	0.05	0.00
Scopulariopsis brevicaulis (Sacc.) Bainie	0.07	0.00
Sordaria fimicola (Roberge ex Desm.) Ces. & De Not.	0.00	0.02
Sporothrix sp. Hektoen & Perkins	0.14	0.15
Stachybotrys chartarum (Ehrenb.) Hughes	0.01	0.01
Syncephalastrum racemosum Cohn ex Schröt.	0.18	0.00
Talaromyces wortmannii Benj.	0.09	0.00
Tiarosporella paludosa (Sacc. & Fiori) Höhn.	0.00	0.01
Torula caligans (Bat. & Upadhyay) Ellis	0.01	0.00
Trichoderma aureoviride Rifai	0.77	1.01
Trichoderma harzianum Rifai	2.83	3.33
Trichoderma koningii Oudem.	0.83	0.73
Trichoderma longibrachiatum Rifai	0.02	0.00
Trichoderma pilulíferum Webster & Rifai	0.88	0.84
Trichoderma pseudokoningii Rifai	0.03	0.00
Trichoderma viride Pers	2.09	1.20
Trichosporon sporotrichoides Oorschot & de Hoog	1.50	0.68
Verticillium chlamydosporium Goddard	0.48	0.05
Wiesneriomyces laurinus (Tassi) Kirk	0.00	0.02
Total	45.03	44.04

matter (DOMSCH et al., 2007).

The identified species are mostly saprophytic, although some act also in the biocontrol of plant diseases and pests. The regular addition of organic matter to the soil and proper handling of its sources, as in agroforestry system, stimulate the activity of primary decomposers, particularly fungi, which are also potential antagonists to plant pathogens (other fungi, insects, nematodes and bacteria) (JANVIER et al., 2007; RAAIJMAKERS et al., 2009).

Agroforestry system soil is home to species of *Trichoderma*. According to Vinale et al. (2008), *Trichoderma* species produce different hydrolytic enzymes and while decomposing organic matter, act in the control of plant pathogens (fungi, bacteria and nematodes), and can promote plant growth. The high incidence of *Trichoderma* in soil may be related to the wide diversity of plant species found in this area. Studies

have shown that T. *harzianum* and T. *viride* are known to have high affinity with the rhizosphere and thrive when there are plenty of healthy roots (YEDIDIA, 1999). These fungal species are attracted by exudates released by the roots.

Purpureocillium lilacinum (syn: *Paecilomyces lilacinus*) showed high density, being the second most abundant species in the agroforestry system (Table 1). In Brazil, there are records of P. *lilacinum* in different types of soil (CAVALCANTI et al., 2006; SCHOENLEIN-CRUSIUS et al., 2006). This species has often been isolated from different hosts or substrates from various locations with worldwide distribution, although more frequently from agricultural soils (DOMSCH et. al., 2007) in which it has been effective for the biocontrol of Meloidogyne (nematodes) species (KHAN et al., 2006; HUANG et al., 2016). This controlling effect is characterized by fungal penetration in the eggs of the nematodes, destroying the embryo. The fungus can also exert strong pressure on the reproductive capacity of females that are first colonized and subsequently killed (CADIOLI et al., 2009).

Entomopathogenic *Beauveria bassiana* and *Metarhizium anisopliae* were also isolated (Table 1). The presence of these fungi aids in the control of pests that cause damages to the system. *Metarhizium anisopliae* infects more than 300 species of insects from different orders, is widely distributed in nature and is found in soils as saprobe, and also colonizing the rhizosphere of plants, which assists in the control of soil insects (TIAGO et al., 2014).

Occurrence of fungal species with potential for the control of organisms that cause damage to crops in agroforestry system is directly related to the adopted management and the high diversity of plant species that seek biological equilibrium.

Soil management and crop can influence population dynamics of soil organisms. Agroforestry systems aim at a productive system with structure, composition, and functioning similar to the local natural vegetation, whose dynamics lead to the restoration of environmental functions and the increase of biodiversity (JOSE, 2012; ARIAS and ABARCA, 2014). The great contribution of litter and nutrients to the soils of the agroforestry systems is a product of its high plant diversity, including its tree component. Different plants present in the soil can form litter of different quantity and quality, which will result in soil differences that determine a greater diversity of niches for the community of decomposers associated to it.

Univariate indices of the filamentous soil fungal community

Univariate indices were estimated from the data in Table 1, isolation of filamentous fungi from the agroforestry soil. In the first and second years of analysis, 96 and 79 species of filamentous fungi were identified, respectively, with 65 common species between the two sampling periods.

The total number of fungal species detected was highly significant, though the rarefaction curve has not reached the asymptote. The accumulation curves of species richness estimators produced by Jacknife 1 and 2 also indicated that there is still a tendency to find more species of filamentous fungi in this agroforestry soil if sampling could be carried on (Figure 1).

The richness found in this work (110 species) represented 79% and 72% of the richness estimated by

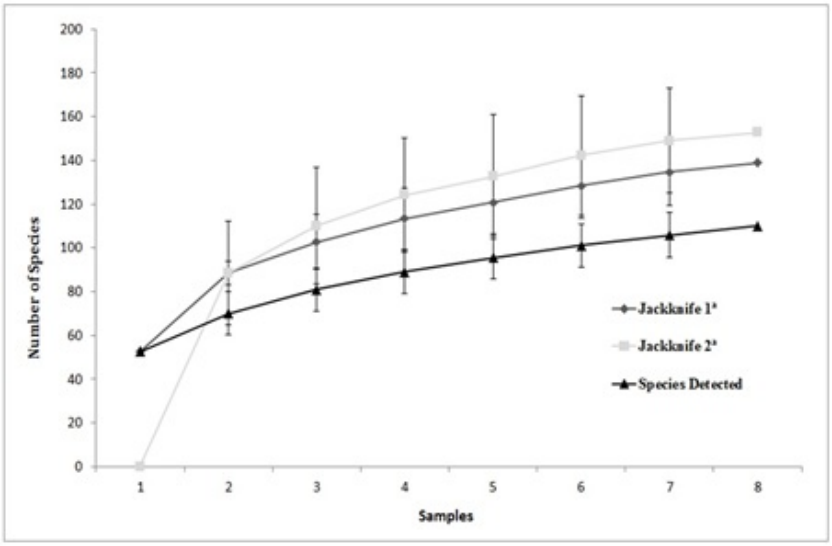

Figure 1. Species of filamentous fungi detected in the agroforestry soil and species accumulation curves estimated by Jacknife 1 and Jacknife 2.

Jacknife 1 and 2, respectively. When the accumulation curve reaches the asymptote, i.e. reaches a point where the increase in sampling effort does not result in increased number of species, one assumes that practically all the richness in the area was sampled. However, curve stabilization is very difficult, especially in tropical regions where many rare species are often added after more samples are taken (COLWELL and CODDINGTON, 1994).

Richness and diversity of species depend on the community type and sampling effort as the number of species is proportional to the number of individuals sampled. In a real community, species have different contributions to the community structure, being impossible to reach maximum evenness (all defined species have equal importance). In a natural environment, most species are rare, with few individuals, while a few species are dominant or common (high importance values), corroborating the results found in this work for filamentous fungi of agroforestry soil (Table 1).

To date, no published study was found estimating the richness of filamentous fungi in agroforestry soils or other soil types (managed or not) in Brazil (COSTA et al., 2012). However, similar results were found for mycorrhizal fungi (AMF). Pereira et al. (2014) evaluated the richness of AMF in areas of Atlantic Forest under different management and were able to recover 70-77% of species present in the areas. Silva et al. (2012) detected 70 to 80% of the estimated AMF species for the areas of salt marsh and sand dunes in Northeast of Brazil.

The fungal diversity index was significantly higher in the first year of this research (Table 2). However, both values are considered high values, close to those reported for forest environments (COSTA et al., 2012).

The diversity of fungi found in agroforestry soil reflects the balance within this system as its great abundance of plant species is responsible for producing a varied layer of plant debris to the soil surface, providing greater depth to the organic layer and higher abundance of fungi that use this material as a major source of energy (RAAIJMAKERS et al., 2009; JOSE, 2012). Thus, a highly diverse fungal community contributes to more efficient use of resources (BERG et al., 2001).

The distribution of isolates among the fungal species showed good uniformity, with an evenness index of 0.82 indicating low species dominance for both study years (Table 2). The soil in the agroforestry system has significant levels of organic matter due to the constant deposition of leaves forming the litter layer (MAIA et al., 2007) thus there is a tendency to maintain more stable

Table 2. Species richness, Shannon-Wiener diversity (H '), Pielou's Equitability (J') and Berger-Parker Dominance of filamentous fungi isolated from agroforestry soil

Index	[1]First Year	[1]Second Year	[2]*Boot p (eq)*
Species richness (S)	96	79	0.001
Shannon-Wiener (H')	3.78	3.59	0.001
Equitability (J')	0.83	0.82	0.278
Dominance (d)	0.08	0.08	0.591

[1] **First year** (August, 2011 to July, 2012) and second year (August, 2012 to July, 2013).

[2] ***Boot* p** (eq): probability of having equal diversities. If p (q) is higher than 0.05, there is no significant difference.

fungal populations throughout the year, probably as a result of richness of ecological niches formed by the heterogeneity of carbon sources.

The fact that no severe disease or pests were observed within the studied agroforestry system has an influence in the production and quality of crops, being related to the favourable development of antagonistic fungi that act in both the process of decomposition of soil organic matter and the suppressiveness of the soil.

Conclusions

The sampling effort was sufficient to isolate approximately 75% of the community of cultivable filamentous fungi from the soil. Thus, it was possible to determine that the diversity and richness of filamentous fungi in this agroforestry soil are high, possibly influenced by the plant diversity that provides different amounts and quality of litter. The composition of the community of filamentous fungi in the agroforestry system soil consists mainly of saprobic fungi that act in the decomposition of organic matter and species with potential for the promotion of plant growth and control of diseases and pests, allowing the exclusion of fertilizers and pesticides for the maintenance of this system of production.

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