Mesofauna assemblages on the extraradical mycelium of *Pinus greggii* roots with three ectomycorrhizal fungi

Ensambles de mesofauna en el micelio extraradical de raíces de *Pinus greggii* con tres hongos ectomicorrízicos

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RESUMEN

Antecedentes: El micelio extraradical (MER) de hongos ectomicorrízicos es una red habitada por mesofauna del suelo, colémbolos y ácaros, formando interacciones durante el ciclo de vida del hongo, desde consumir hifas hasta dispersar esporas. Sin embargo, se desconoce si el MER podría influir en ensamblajes de la mesofauna.

Objetivos: Evaluar la abundancia y composición de las comunidades de mesofauna que habitan en el MER de *Hebeloma mesophaeum*, *Laccaria laccata* y *Wilcoxina* sp. en raíces de *Pinus greggii*.

Métodos: La mesofauna fue colectada en cepellones de *P. greggii* con 80 % de colonización, utilizando un método de lavado.

Resultados y conclusiones: Se observó un efecto por las diferencias del MER sobre la riqueza y dominancia de especies, pero no sobre la abundancia y composición de las comunidades de mesofauna; *Wilcoxina* sp. presentó la menor riqueza de especies. Los colémbolos fungívoros formaron ensambles de especies de isotomidos-tullbergidos que habitan en el suelo. Los Entomobryidae e Hypogastruridae fueron las familias comunes sobre la superficie del suelo, éstas no fueron encontradas en *Wilcoxina* sp. Pocos ácaros depredadores (Mesostigmata y Endeostigmata) fueron encontrados. El micelio ectomicorrízico es un nicho trófico de la mesofauna y podría ser una fuerza evolutiva en estructurar la diversidad de especies.

Palabras clave: Acari, Collembola, hifas ectomicorrízicas, interacciones, microartrópodos edáficos

ABSTRACT

Background: The extraradical mycelium (ERM) of ectomycorrhizal fungi is a network inhabited by soil mesofauna, mainly collembolans and mites, forming interactions during the fungal life-cycle, from grazing on hyphae to spore dispersal. However, it is still unknown if ERM of ectomycorrhizal fungi could influence the structure of mesofauna assemblages.

Objective: To evaluate the abundance and community composition of the mesofauna inhabiting the ERM of *Hebeloma mesophaeum*, *Laccaria laccata* and *Wilcoxina* sp. in *Pinus greggii* roots.

Methods: Mesofauna was collected from the root balls of *P. greggii* with 80 % of colonization using a washing method.

Results and conclusions: An effect was observed due to ERM differences on species richness and species dominance, but not an effect on the abundance and community composition of the mesofauna. However, *Wilcoxina* sp. presented the lowest species richness and diversity. Fungus-feeding collembolans shaped species-rich assemblages, being isotomid-tullbergid forms the soil-dwelling taxa. Entomobryidae and Hypogastruridae were the most common families on the soil surface, not being found in *Wilcoxina* sp., and only a few predatory mites of the Mesostigmata and Endeostigmata were found. The ectomycorrhizal mycelium constitutes a trophic niche of the mesofauna and it might be an evolutionary force in structuring species composition and diversity.

Keywords: Acari, Collembola, ectomycorrhizal hyphae, edaphic microarthropods, interactions

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INTRODUCTION

Ectomycorrhizal symbiosis is one of the most important mutualistic relationships established by forest tree roots and fungi (Smith and Read 2008). The extraradical mycelium (ERM) is the part more closely in contact with the soil (Leake *et al*. 2004) connecting two environments, the plant roots and the surrounding soil (Jansa *et al*. 2013). The mycorrhizal hyphae extending into the soil are exposed to a great number of diverse biotic interactions (Jansa and Gryndler 2010). However, the relationship between soil fauna diversity and mycelium has been poorly studied. It is well known that the hyphae attract diverse soil mesofauna composed by a wide range of highly abundant life-forms, accounting for about 85 % of the microarthropods in forest soils (Hope 2003). The mesofauna includes mites and collembolans among others, having important roles in the decomposition of organic matter, carrying out the initial fragmentation and comminution of litter (Swift *et al*. 1979; Petersen and Luxton 1982; Seastedt 1984; Orgiazzi *et al*. 2016; Frouz 2018) and transforming ingested plant debris into humus-rich fecal pellets that improve soil structure (Cassagne *et al*. 2003; Maaß *et al*. 2015).

Interactions between ectomycorrhizal mycelium and soil mesofauna are far more complex than that of consumer-resource interaction, being evidently mutualistic (Hernández-Santiago *et al*. 2020). These interactions can be seen during all mycorrhizal fungal life-cycle, from spore dispersal dynamics to direct stimulus to fungal growth by grazing mycelium (Fitter and Garbaye 1994; Crowther *et al*. 2011); fungivory is widespread among soil invertebrates (Ruess and Lussenhop 2005; Bokhorst and Wardle 2014). However, fungivores show feeding preferences between different groups of fungi (Visser and Whittaker 1977; Hiol *et al*. 1994; Schneider *et al*. 2005; Hernández-Santiago *et al*. 2020) and can be highly selective when foraging on soil fungi (Jørgensen *et al*. 2003; Jørgensen *et al*. 2005; Bluhm *et al*. 2019). The mesofauna also feed on sporomes, having a direct effect on spore dispersal (Behan and Hill 1978; Lilleskov and Bruns 2005; Hernández-Santiago *et al*. 2020); a very efficient spreading mechanism for taking advantage of the searching behavior of microarthropods to reach new sites (Deacon 2006).

The interactions between ectomycorrhizal mycelium and mesofauna have been mainly studied under controlled laboratory conditions. Under this approach, the studies of Hiol *et al*. (1994), who examined *in vitro* culture, the feeding preferences of *Proisotoma minuta* on ectomycorrhizal fungi, demonstrated that these varied among ectomycorrhizal species. On the other hand, Schneider *et al*. (2005) showed that feeding preferences significantly differed between oribatid mite species and that they preferentially selected dark-pigmented fungi (Mitchell and Parkinson 1976; Maraun *et al*. 1998; Schneider and Maraun 2005) over hyaline fungi when both types were offered as food items (Mitchell and Parkinson 1976). According to Fogel (1988), much of the research about soil biota-fungi interactions has focused on host-pathogen interactions rather than on their role in ecosystem processes.

Ectomycorrhizal inoculation is a simple and reliable technology used in Mexico during the last two decades, using ground pilei of edible ectomycorrhizal mushrooms to inoculate forest tree species (Pérez-Moreno et al. 2019, 2020). Inoculation with a specific ectomycorrhizal fungus, such as those of the genus *Hebeloma* and *Laccaria* (Carrasco-Hernández *et al*. 2011, 2015; Martínez-Reyes *et al*. 2012) on pine roots, could be a reliable way to study if the ERM of a single ectomycorrhizal fungal species may influence mesofauna assemblages; this can be achieved by analyzing the ectomycorrhizal roots. In general, the relationship between ERM and mesofauna has received little attention, despite its paramount importance for ecological functions in forests ecosystems. The aim of this study was to evaluate the abundance and community composition of the mesofauna inhabiting the ERM associated to *Pinus greggii* ectomycorrhizal roots inoculated with three different ectomycorrhizal fungi. We raise the hypothesis that there is an effect of the type of ectomycorrhizal mycelium on the soil mesofauna assemblages. Additionally, we evaluated the feeding preferences of collembolans and mites among the ectomycorrhizal species and their trophic niches in relation with their life forms according to Potapov *et al*. (2016).

MATERIALS AND METHODS

Plant material and inoculum
This study was conducted under greenhouse conditions in the nursery facilities at the Colegio de Postgraduados in Montecillo, State of Mexico, Mexico. We

used trees from an ectomycorrhizal inoculation experiment established by Martínez-Reyes *et al.* 2010. The *Pinus greggii* Engelm. ex Parl. was selected because it is an endemic Mexican pine that grows in the Sierra Madre Oriental, being abundantly used in Mexico´s reforestation programs (Ramírez-Herrera *et al.* 2005). The *P. greggii* seeds, used for sowing, were collected from native forests located in the Nevado de Toluca National Park, in the State of Mexico. *Laccaria laccata* s.l. (Scop.) Cooke and *Hebeloma mesophaeum* s.l. (Pers.) Quél. were the two edible ectomycorrhizal fungi used to inoculate *P. greggii*; these species are early colonizers (Nara *et al.* 2003; Obase *et al.* 2007) and grow in low fertility conditions (Trocha *et al.* 2007).

The accurate description of the morphology of the morphotypes of the studied species has already been published by Carrasco-Hernández *et al.* (2011, 2015) and Martínez-Reyes *et al.* (2012) as well as their molecular characterization; GenBank accession numbers KY969630 and MF034059 for *L. laccata* and *H. mesophaeum*, respectively. The sporomes used as source of inoculum were purchased in the local market of Ozumba, in the State of Mexico; the wild mushrooms were collected from San Pedro Nexapa forests, State of Mexico. The spore inoculum was obtained from the pilea of sporomes, being cut from the stipe, and dehydrated at 35 °C for 48 hours; finally, grinded and sieved to homogenize the inoculum particle size (see Carrasco-Hernández *et al.* 2011; Martínez-Reyes *et al.* 2012 for the full inoculation method). *Wilcoxina* sp. is an abundant ectomycorrhizal fungus with dark brown mycelium that does not produce fruiting bodies and commonly colonizes pine roots in native forest of Central Mexico.

In this study, it was included a dark brown ectomycorrhizae due to the fact that collembolans and oribatid mites preferentially feed on dark pigmented fungi (Mitchell and Parkinson 1976), such as those of the Dematiaceae family (Maraun *et al.* 1998; Schneider and Maraun 2005). However, it has not yet been reported whether dark-brown ectomycorrhizal mycelium might be a food resource to mesofauna.

Setting up of the experiment and experimental design

The experiment was set up using tree pots of 5.5 x 18 cm (diameter x height) and 320.7 cm^3 of capacity. A mixture of sand, bark and forest soil in a 2:2:1 ratio was used as substrate, which was sterilized with steam

for three hours, then after 24 hours the process was repeated (Martínez-Reyes *et al.* 2012), prior to fill the tree pots. Seeds were sterilized with 30 % H_2O_2 for 20 minutes and rinsed four times with sterile distilled water, before being directly planted in the containers with the substrate described above. Once the *P. greggii* seeds germinated and produced their first true leaves, 36 days after sowing, they were inoculated. A second inoculation dose was applied 90 days later (for details, see Carrasco-Hernández *et al.* 2011; Martínez-Reyes *et al.* 2012). In total each plant received 10^7 to 10^8 spores of *H. mesophaeum* or *L. laccata*, contained in 3 g of dry inoculum. Spore inoculum concentration counting was carried out by using a Neubauer chamber (Marienfeld, Lauda-Königshofen, Germany) following Rentería-Chávez *et al.* (2017).

The inoculation method used for *Wilcoxina* sp. was different compared to that used for the other two ectomycorrhizal fungi. This was based on the fact that *Wilcoxina* sp. abundantly colonizes the roots of *Pinus ayacahuite* and the sampling of ectomycorrhizas of this fungus is quite easy due to its characteristic morphoanatomical features, including their characteristic dark-brown mycelium with a high mycelial density which form mycelial patches and their simple straight morphotypes (Figure 1) (DEEMY 2018); in contrast, this fungus does not produce visible ascomata.

Thus, the inoculum source for *Wilcoxina* sp. consisted in 10 g of ectomycorrhizal root tips collected in a *Pinus ayacahuite* stand located in the Monte Tlaloc, San Pablo Ixayoc, Texcoco, State of Mexico. Previously, it was carried out morphological and molecular identification of *Wilcoxina* sp. in this forest stands (Carrera-Martínez 2017). As the final goal was to produce heavily colonized mycorrhizal plants, the different inoculation techniques used to produce them, did not affect the study rationale.

The treatments consisted in inoculating *Pinus greggii* with the ectomycorrhizal fungi: i) *Hebeloma mesophaeum*; ii) *Laccaria laccata* and iii) *Wilcoxina* sp. were kept in different growing support trays, in order to avoid cross-contamination. After six months of colonization, the seedlings were arranged in a completely randomized experimental design with 3 treatments and 7 replicates per treatment, having a total of 21 experimental units, each one consisting in an inoculated tree. The twenty-one seedlings were maintained for 7 years, all of them survived.
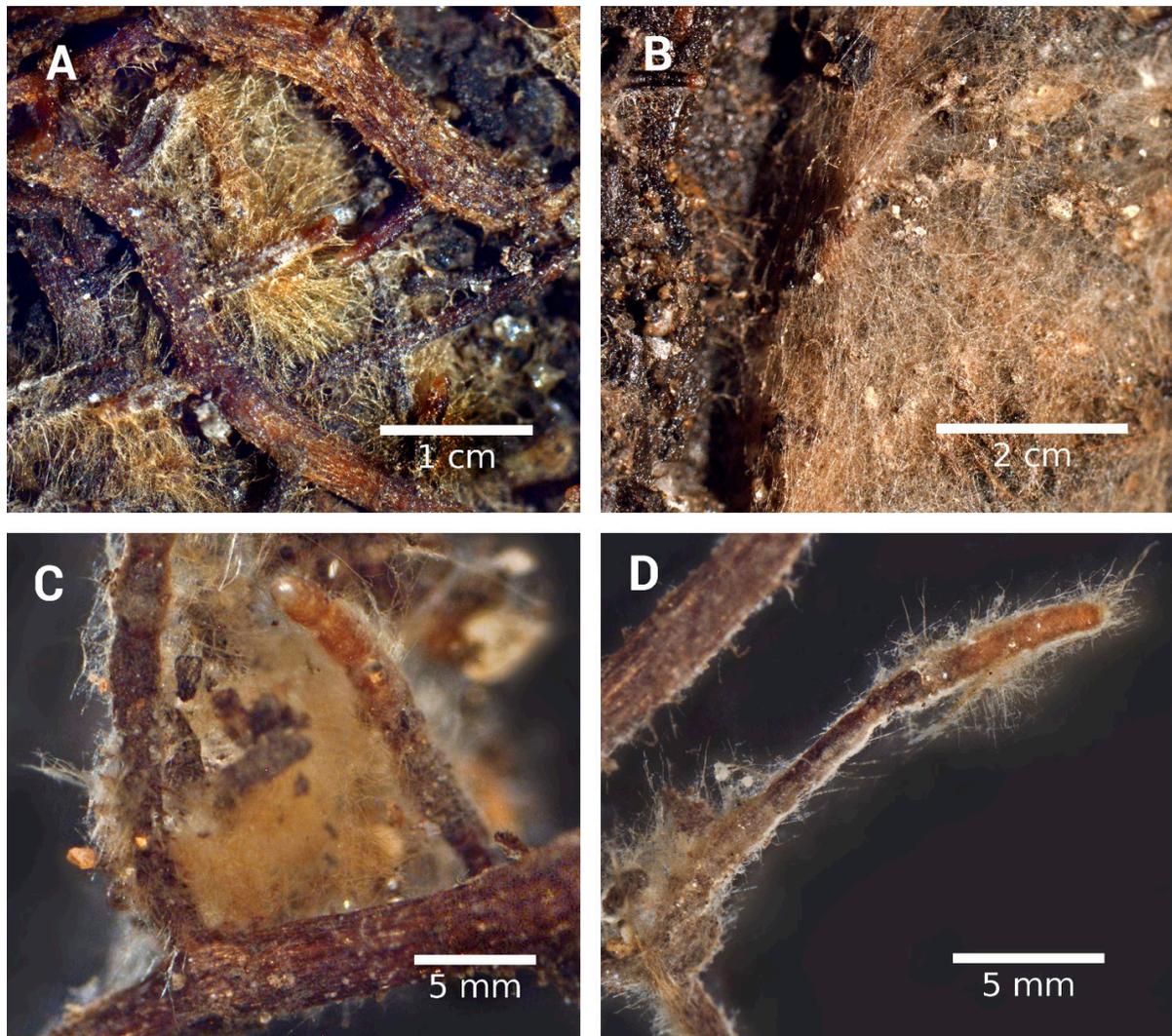
Figure 1. Morphological characterization of *Wilcoxina* sp. A: Mycelial patch. B: A close up of dark-brown external mycelium. C and D: Simple straight morphotypes.

The maintenance of this period of time is related with the fact that *Wilcoxina* sp. external mycelium is known to grow very slowly. After this time, a meticulous analysis was conducted in order to determine the colonization percentage of ectomycorrhiza and the external mycelium development in all plants. This analysis showed that ectomycorrhizal colonization and external mycelium development was quite variable among experimental units. Thus, in order to made valid comparisons among treatments, only those plants having at least 80 % of ECM colonization and the external surface of the root balls completely covered with external mycelium of the inoculated fungi were selected; morphotyping was carried out following DEEMY (2018). Only 3 replicates per treatment filled the two requested criteria mentioned above.

Mesofauna extraction and identification

Mesofauna was collected from the root balls of three replicates per treatment selected as mentioned above, using a modification of the washing method of Karasawa and Hijii (2005). The root ball was cut into 4 pieces and each piece was immersed in a plastic container with tap water (ca. 1L). Roots with mycelium were washed to remove the soil and the soil solution was stirred several times for 2 hours and then filtered using stainless steel meshes; collembolans and mites were trapped by the 0.15 mm-mesh sieve and stored in vials containing 70 % ethanol. Mesofauna were separated and sorted under a Zeiss Stemi DV4 stereo microscope. For species identification, morphotypes were previously cleared with 85 % lactic acid or lactophenol solution before mounting in Hoyer's

medium and slices were dried at 45 °C for 4-5 days, using a drying oven; mounted specimens were identified to genus or species level under a phase contrast microscope (Zeiss Axiostar Plus). Collembolans were identified using the keys of Christiansen and Bellinger (1998) and Bellinger *et al*. (1996-2018) and mites according to a manual of acarology (Krantz and Walter 2009).

Statistical analysis

Abundances of mesofauna expressed as the total number of individuals per tree pot (320.7 cm^3) were used to estimate the total abundance of mites and collembolans that inhabited on the ERM of *P. greggii* ectomycorrhizal roots inoculated with the three fungal species described above. Abundances were analyzed with a completely randomized design with 3 treatments and 3 replicates per treatment with perANOVA (permutational analysis of variance) and a level of significance of α=0.05; Monte Carlo *p*-values (pmc). This is an approach to avoid problems with non-normal data and unequal variances and to use with one variable response (Anderson 2005). PerANOVA was based on Euclidian distance and ectomycorrhizal species as fixed factor, and was carried out in PERMANOVA software version 1.6; which is a FORTRAN computer program for testing ANOVA experimental designs on the basis of distance measurements using permutation methods (Anderson 2001, 2005). Before statistical analysis, data were log-transformed ($x'= \log(x)$).

Individual-based rarefaction curves were used to compare species richness among the mesofauna inhabiting the ERM of the three ectomycorrhizal species. Because richness increases with sample size, rarefaction computes comparable species richness adjusted for the same number of individuals collected, which will be the total abundance for the smallest of the assemblages (Colwell *et al*. 2012); this is also referred to as sampling effort standardized for comparable levels of abundance (Buddle *et al*. 2005). The pooled abundance data, based on all the species found, in each ectomycorrhizal fungi was used to compute the rarefaction estimates using the 'vegan' package in R statistical software version 3.2.5 (R Development Core Team 2016).

Permutational Multivariate Analysis of Variance (PERMANOVA Anderson 2001) was used to test the null hypothesis of no difference in the soil mesofauna communities due to the effect of ectomycorrhizal fungus.

This analysis was performed in PERMANOVA v.1.6 (Anderson 2005) based on one-way design and using Bray-Curtis dissimilarity distance measure and the test of significance (α = 0.05) estimated after 9999 unrestricted permutations. Hellinger-transformed species data was used because it allows comparisons among samples with varying sampling effort and also reduces the effect of several very abundant species keeping the variations in relative species composition per sample (Borcard *et al*. 2011).

Species-dominance metric as defined by Pinzón and Spence (2010) was computed to show the degree of dominance or commonness of the total number of species found in the mycelium of the three ectomycorrhizal species. The dominance value (DV) was calculated for each species as a product of the relative proportional abundance (w) and proportional presence (AP) and then being relativized each of the obtained values with respect to the total sum of all DV values, resulting in a relative dominance value (DV') for each species in the assemblage. Additionally, the sum of all dominance values is 1.0 (or 100 %) and therefore the more abundant and frequent the species is in relation to the other species in the assemblage, the closer its dominance value (DV') is to 1.0. According to a dominance plot, thresholds have been defined for dominant (Dom), subdominant (SubD), common (Com) and uncommon (UCom) species.

RESULTS

Mesofauna abundances

A total of 680 individual mites and collembolans, including 7 families, 12 genera and 15 species were identified in the present study (Table 1). Of these, 301 individuals of 11 species were collected from the ERM of *L. laccata*, 130 individuals of 9 species from *H. mesophaeum*, and 249 individuals of 6 species from *Wilcoxina* sp. (Table 1); twelve species belonging to Collembola (91.6 %) and only three species to Acari (8.4 %). The most abundant collembolans were *Mesaphorura florae* (59.6 %), *Hemisotoma thermophila* (15 %), *Proisotoma subminuta* (6.5 %) and *Mesaphorura yosiii* (5.7 %). Only mites of the order Mesostigmata and suborder Endeostigmata were found in the mycelium of the three species of ectomycorrhizal fungi, being identified *Protogamasellus mica* (5 %), *Alicorhagia usitata* (3.1 %) and *Asca garmani* (0.3 %).

Although there was no statistical difference among mesofauna abundances (pseudo-$F_{[2,6]}$=0.799, *p*=0.5031), the highest average abundance of mesofauna was found in *L. laccata* (100 individuals per 320.7 cm³), intermediate in *Wilcoxina* sp. and the lowest abundances in *H. mesophaeum* (83 and 43 individuals per 320.7 cm³, respectively). The lack of statistical significance among the different abundance values was probably due to the high dispersion of the total number of individuals captured in each root ball sampled. The largest within-root balls abundance variation was observed with *Wilcoxina* sp. (Figure 2), most likely as a result of the high density of hyphae that it produces (Figure 1b) and the sample size (n=3).

Species richness

Species richness curves followed an curvilinear shape which was a good indication of appropriate sampling to make reliable comparisons of species richness (Buddle *et al.* 2005; Colwell *et al.* 2012) among the mesofauna that lived on the ERM on the roots of *P. greggii* inoculated with *L. laccata*, *H. mesophaeum* and *Wilcoxina* sp.
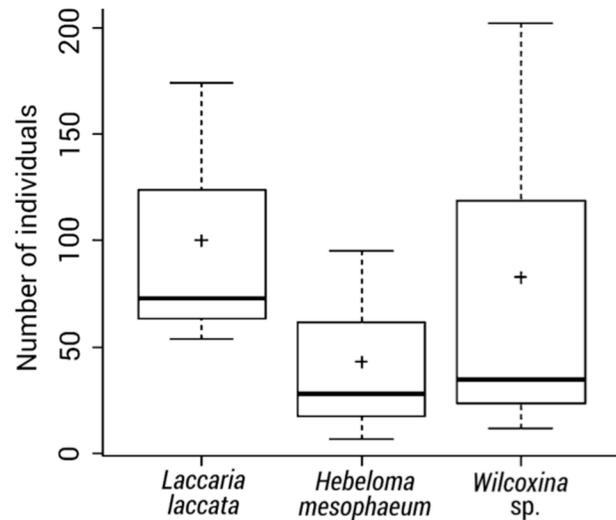
Figure 2. Abundances of Collembola and Acari found in the extraradical mycelium of *Pinus greggii* roots with three ectomycorrhizal fungi: *Laccaria laccata*, *Hebeloma mesophaeum* and *Wilcoxina* sp., expressed as number of individuals per tree pot (320.7 cm³). Note: The plus sign (+) indicates the average abundance (n=3).

Table 1. Relative abundances of mesofauna (collembolans and mites) from the extraradical mycelium of *Pinus greggii* of three species of ectomycorrhizal fungi: *Laccaria laccata*, *Hebeloma mesophaeum* and *Wilcoxina* sp., under greenhouse conditions

High taxonomic rank	Family	Species name	*Laccaria laccata*	*Hebeloma mesophaeum*	*Wilcoxina* sp.
Class Collembolla					
Order Poduromorpha	Tullbergiidae	*Mesaphorura florae* (Simon, Ruiz, Martin & Luciañez, 1994)	36.8 (16.5)	71.6 (4.2)	65.5(11.9)
		Mesaphorura yosiii (Rusek, 1967)	0.0 (0.0)	0.0 (0.0)	6.4 (6.4)
		Mesaphorura iowensis (Mills, 1932)	0.6 (0.6)	0.0 (0.0)	0.0 (0.0)
	Hypogastruridae	*Mitchellania* ca. *vulgaris*	0.2 (0.2)	2.8 (2.8)	0.0 (0.0)
		Ceratophysella ca. *gibbosa*	0.0 (0.0)	0.4 (0.4)	0.0 (0.0)
		Hypogastrura ca. *harveyi*	0.0 (0.0)	0.7 (0.7)	0.0 (0.0)
		Schoettella distincta (Denis, 1931)	0.0 (0.0)	0.4 (0.4)	0.0 (0.0)
Order Entomobryomorpha		*Hemisotoma thermophila* (Axelson, 1900)	20.8 (14.0)	2.6 (1.3)	1.0 (1.0)
	Isotomidae	*Proisotoma subminuta* (Denis, 1931)	16.6 (14.4)	7.4 (3.5)	20.5 (15.1)
		Proisotoma minima (Absolon, 1901)	10.5 (10.5)	0.0 (0.0)	0.0 (0.0)
		Lepidocyrtus sp.	0.6 (0.6)	0.0 (0.0)	0.0 (0.0)
	Entomobryidae				
Order Neelipleona		*Megalotorax perspicillum* (Schneider & D'Haese, 2013)	0.6 (0.6)	0.0 (0.0)	0.0 (0.0)
	Neelidae				
Subclass Acari					
Order Mesostigmata		*Protogamasellus mica* (Athias-Henriot, 1961)	8.6 (3.5)	6.0 (4.3)	2.9 (2.9)
	Ascidae	*Asca garmani* (Hurlbutt, 1963)	1.1 (0.6)	0.0 (0.0)	0.0 (0.0)
Suborder Endeostigmata		*Alicorhagia usitata* (Theron, Meyer & Ryke, 1970)	3.5 (2.0)	8.3 (8.3)	3.8 (2.4)
	Alicorhagiidae				
Total*	7	12	15	11	9	6

*Total number of families, genera or species recorded. Note: Relative abundance values are means (n = 3) and standard error given in parentheses.

Rarefied species richness was standardized by the mi-nor number of individuals collected, which was 130 in-dividuals, to allow meaningful comparisons of species richness and to take into account sampling effort (Bu-ddle *et al.* 2005). The rarefaction curves showed that species richness was lowest in *Wilcoxina* sp. (5 spp.) compared to *L. laccata* and *H. mesophaeum*, both of which recorded the highest richness (8 spp.); thus, no differences were detected between these two ectomy-corrhizal fungi (Figure 3). These estimates suggest a relationship between the species richness of mesofau-na and the morphological characteristics of the mycelia of the ectomycorrhizal species where the mesofauna inhabited.

Effect of ectomycorrhizal fungi on species dominance

An initial ordination of the species data indicated no differences in species composition because there was no 2-dimensional arrangement of the points (results not shown). PERMANOVA analysis showed no effect on the community composition of the mesofauna due to influence of the ectomycorrhizal specie ($F_{[2,6]}$=1.07, p=0.406). Species dominance analysis supported PER-MANOVA results indicating the presence of one hi-ghly dominant collembolan species in the root balls, *Mesaphorura florae* with a relative dominance value of DV'=73.50 (Figure 4); which may directly influence that there were no significant differences among the mesofauna communities that dwelled on the ERM of *L.*

laccata, *H. mesophaeum* and *Wilcoxina* sp.; the com-munity structure is a function of the number and re-lative abundances of species in a habitat (Starr *et al.* 2016). Furthermore, the subdominant species were *Hemisotoma thermophila* and *Proisotoma subminuta* having relative dominance values of (DV'=12.34) and (DV'=6.21), respectively, as well as, *Protogamasellus mica* (DV'=4.11) and *Alicorhagia usitata* (DV'=2.12) were subdominant species belonging to Acari. Al-though a reduced number of species were common or uncommon, it was shown that they had a particu-larly preference for dwelling in a specific ectomycorr-hizal mycelium. For instance, *Mitchellania* ca. *vulgaris* (DV'=0.36) and *Hypogastrura* ca. *harveyi* (DV'=0.04) mostly inhabited in the ERM of *H. mesophaeum* and *Mesaphorura yosiii* (DV'=0.79) dwelled in *Wilcoxina* sp. The predator mite *Asca garmani* (DV'=0.08) and the collembolans such as *Proisotoma minima* (DV'=0.34) and *Mesaphorura iowensis* (DV'=0.02) were uncom-mon *L. laccata*-dwelling species. Subdominant and un-common species may influence the results of species richness of the mesofauna that inhabited on the ERM of each ectomycorrhizal fungus.

DISCUSSION

In this paper, we attempted to define if the ectomy-corrhizal mycelium may influence mesofauna assem-blages because it is unknown the dynamics involved
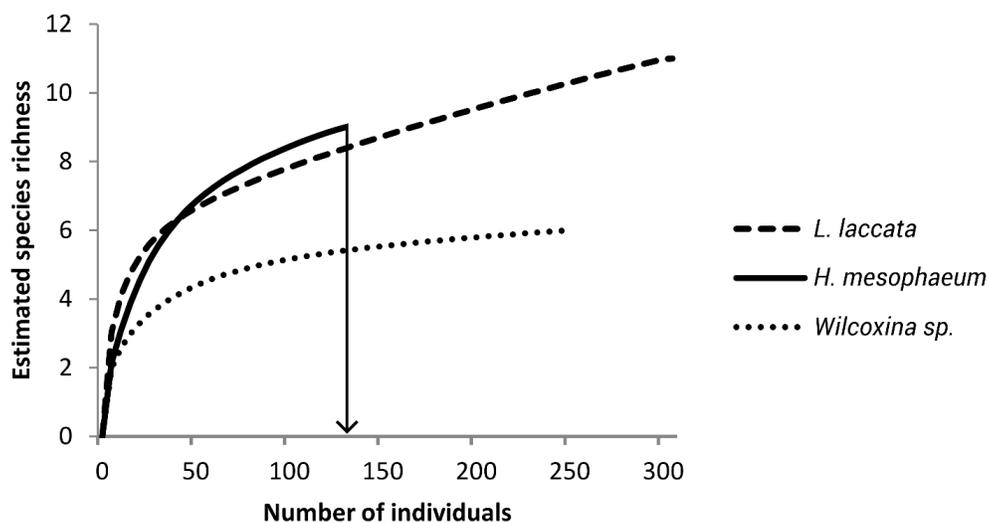
Figure 3. Individual-based rarefaction curves of estimated species richness of Collembola and Acari from the extraradical mycelium of *Pinus greggii* roots with three ectomycorrhizal fungi: *Laccaria laccata*, *Hebeloma mesophaeum* and *Wilcoxina* sp.; the estimation was standardized by minimum sample size of 130 individuals indicated by the arrow.
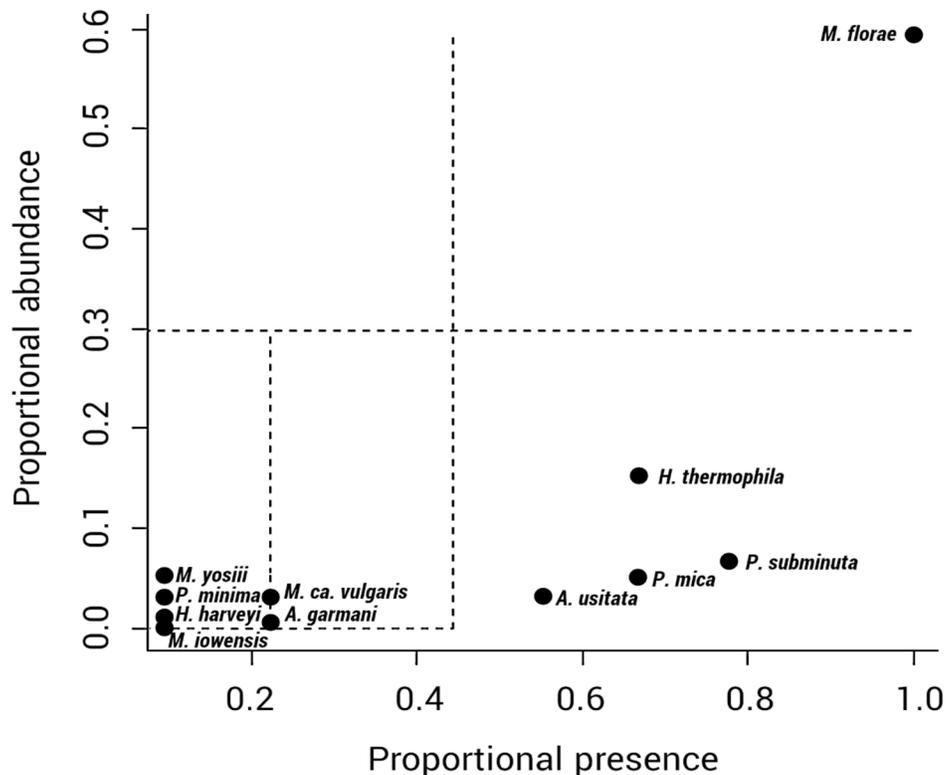
Figure 4. Dominance plot of all mesofauna (collembolans and mites) found in the extraradical mycelium of the roots of *P. greggii* with three ectomycorrhizal fungi: *L. laccata*, *H. mesophaeum* and *Wilcoxina* sp. Note: Dominant species in the upper right quadrant and subdominant species in the lower right quadrant. In the lower left quadrant, common species on the right and uncommon species on the left.

during the assembly processes and if ERM could provide unique biotic and abiotic characteristics to mesofauna that colonize it. In general, the results do not support our hypotheses that expected an effect on the abundance and community composition of mesofauna assemblages inhabiting on the ERM of three different ectomycorrhizal species. However, we did observe an effect on species richness and species dominance, of the total number of mesofauna species found in the three ectomycorrhizal fungi. A fully structured mesofauna assemblage naturally associated with the ERM of *L. laccata*, *H. mesophaeum* or *Wilcoxina* sp. was not observed because the mesofauna colonization process could be more slowly in the tree pots than in a natural environment.

On the other hand, in his microcosm experiment Setälä (1995) defaunated and reinoculated with diverse soil fauna seedlings of *Pinus sylvestris* infected with different ectomycorrhizal fungi, obtaining an abundant and taxonomically diverse mesofauna to evaluate the impact of soil fauna on ectomycorrhizal biomass. However, the goal of this study was to know if the co-

llembolans and mites could choose for themselves an ectomycorrhizal species which could provide them an adequate habitat and food resources. A surprising notable absence was that of oribatid mites, constituting one of the major litter dwelling mycophagous that feed on ectomycorrhizal and saprotrophic fungi (Schneider *et al*. 2005; Schneider and Maraun 2005). In this regard, Booth and Swanton (2002) mentioned that dispersal constrains determine what species arrive at a site. In this study, it was assumed that there was a continuous arrival of collembolans and mites at the tree plots; however, this was not the case for oribatid mites, considering their low dispersal ability (Lebrun and van Straalen 1995), they could not colonize the tree pots. Whereas collembolans rapidly expanded their distribution, especially for their dispersal ability and high reproduction rates.

According to Maharning *et al*. (2009) the two factors that influence the soil communities are the nutrient resources available and the microhabitat diversity as well as the trophic niches related to taxonomic identity and life forms (Potapov *et al*. 2016). Collembolans

such as the genera *Mesaphorura*, being characterized as soil-dwelling (euedaphic) taxa, were the most abundant dwellers (Table 1). Stebaeva (1970) and Potapov *et al.* (2016) indicated that adaptations to dwelling in deeper soil layers are expressed by minute body length, lack of pigmentation, no eyes, furcula absent and short legs. The degree of occurrence was confirmed by the high abundance and presence of the *Mesaphorura* species in the tree pots; therefore, isotomid-tullbergid collembolans are the most closely related to inhabit the soil and mycelium. Adaptations to life on the surface of soil (epedaphic species) were evidenced for the presence of species of the Entomobryidae and Hypogastruridae families; these collembolans were of large to medium-size, with furcula, frequently pigmented and with ocelli (Potapov *et al.* 2016). However, they were not dwellers in *Wilcoxina* due to habitat restrictions such as non-formation of sporomes.

Effect of the ectomycorrhizal fungi on mesofauna species richness

Assessment of the three ectomycorrhizal fungi *L. laccata*, *H. mesophaeum* and *Wilcoxina* sp. clearly showed that the ERM have an effect on species richness. Changes in species richness may reflect the habitat availability associated with the different mycelial morphology which is highly dependent on the intrinsic genetics of the ectomycorrhizal fungi. For example, the low species richness from the dark mycelium of *Wilcoxina* could be related to high density, thickness or tangled mass of hyphae that form its mycelium in comparison with less dense hyphal strands of *L. laccata* and *H. mesophaeum*. Previously, it has been demonstrated that the extent and structure of ERM differ among ectomycorrhizal fungal taxa, particularly in terms of emerging hyphae and rhizomorphs (Agerer 2001). From the viewpoint of mesofauna distribution in this study, it seem to be unevenly distributed among the three ectomycorrhizal mycelia and, at the same time, *L. laccata* and *H. mesophaeum* mycelia hosted quite different species of collembolans (Table 1). The higher species richness shared by *H. mesophaeum* and *L. laccata* highlights the importance of the low mycelial density and hyaline mycelium to support higher species richness compared to *Wilcoxina* treatment, which had abundant dark brown external mycelium which frequently forms mycelial patches. Our results revealed that a higher mesofauna diversity dominated on the

hyaline mycelium of edible ectomycorrhizal species in comparison with that on the dark brown mycelium of ectomycorrhizal fungi.

On the other hand, *H. mesophaeum* showed higher abundance of epedaphic species, corresponding to upper-litter dwellers such as *Lepidocyrtus* sp. and species of the family Hypogastruridae (Stebaeva 1970; Potapov *et al.* 2016), this take place with the apparition of the sporomes. It was found that *Mitchellania* ca. *vulgaris* showed spores in their digestive tract as evidence of feeding on the sporomes produced in the tree pots (Figure 5) and of participating actively in the dissemination of spores. It may be that *Wilcoxina* sp. did not present a higher diversity because it does not produce epigeous fruiting bodies. Our results indicate that the taxonomical composition of the mesofauna richness may be a result in terms of nature of mycelium and of fungal production of sporomes but not in terms of the ectomycorrhizal species. These findings may be considered an unknown ecological phenomenon as no previous research has identified the role of the ERM ectomycorrhizal fungi contributing to differences in mesofauna species richness. Increasing species richness leads to an increase of diversity and ecosystem functioning. However, future research in this area is needed to have more detailed evidence about the factors that influence the formation of mesofauna community structure due to the mycelium of ectomycorrhizal species.

Dominance structure of mesofauna associated to ectomycorrhizal mycelium

Our appreciation of other roles of the ERM is hampered by a lack of understanding of mycelial systems. The mycelial network provides useful insights into the food web dynamics and life forms of mesofauna inhabiting the ERM and these can be viewed analyzing the dominance structure of mesofauna. In this study, we can assume that the degree of mesofauna aggregation in the sampled tree pots was related to the morphology of mycelium creating habitats, which allow the dwelling of species of different trophic niches. The observed presence of collembolan and mite species from the mycelium of the three ectomycorrhizal fungi within the different quadrants of the dominance plot (Figure 4) can be explained by species behavior and life forms. The number of taxa of collembolans (saprophages and mycophages) and predaceous mesostigmatic and endeostigmatic mites in general pre-

dominated during the development of the mycelium; collembolans were by far the most numerous colonizers.

In an immigration test plots, Dunger *et al.* (2002) proved that *Mesaphorura florae* has been transported by air and that it could form stable populations after 4 months and show a noticeable proliferation, being registered as an early colonizers and as a of the dominant species in the plots. Similarly, but in this case under greenhouse conditions, it was found that *M. florae* was the dominant species (Figure 4) and it was considered as the species that first colonized the mycelium. Our findings tend towards the presumption that *M. florae* was the pioneer species with a rapid propagation and that it is able to survive in the ERM of the three ectomycorrhizal fungi. The other possible initial colonizers, *Proisotoma subminuta*, was also present in the three ectomycorrhizal mycelia but with a much lower abundance. The two species showed high abundance on the ERM and this was related to their life forms corresponding to the euedaphic group (Stebaeva 1970). On

the contrary, *P. minima* had only preference for dwelling on the mycelium of *L. laccata* (Table 1). Grazers of the fungal food chain are fungus-feeding collembolans, which shape species-rich assemblages (Scheu and Setälä 2002) and they were mainly found in this study due to formation of functional groups, which implies that collembolans are grouped according to their taxonomic identity, life forms and food sources (Potapov *et al.* 2016). For example, the species of the genus *Mesaphorura* were commonly viewed consuming large quantities of detritus (Figure 6a and 6b) but also are fungal hyphae feeders (Ponge 2000), corresponding to euedaphic species (Potapov *et al.* 2016). *Lepidocyrtus* sp. showed mycelial hyphae of *L. laccata* in its digestive tract (Figure 6c and 6d), despite living preferentially near the surface (epedaphic) (Stebaeva 1970; Potapov *et al.* 2016). The species of Hypogastruridae were the other upper-litter dwellers (epedaphic) that showed gut contents composed mainly of spores, being associated as potential spore-dispersers for dwelling on the fruit bodies of *H. mesophaeum* (Figure 5).
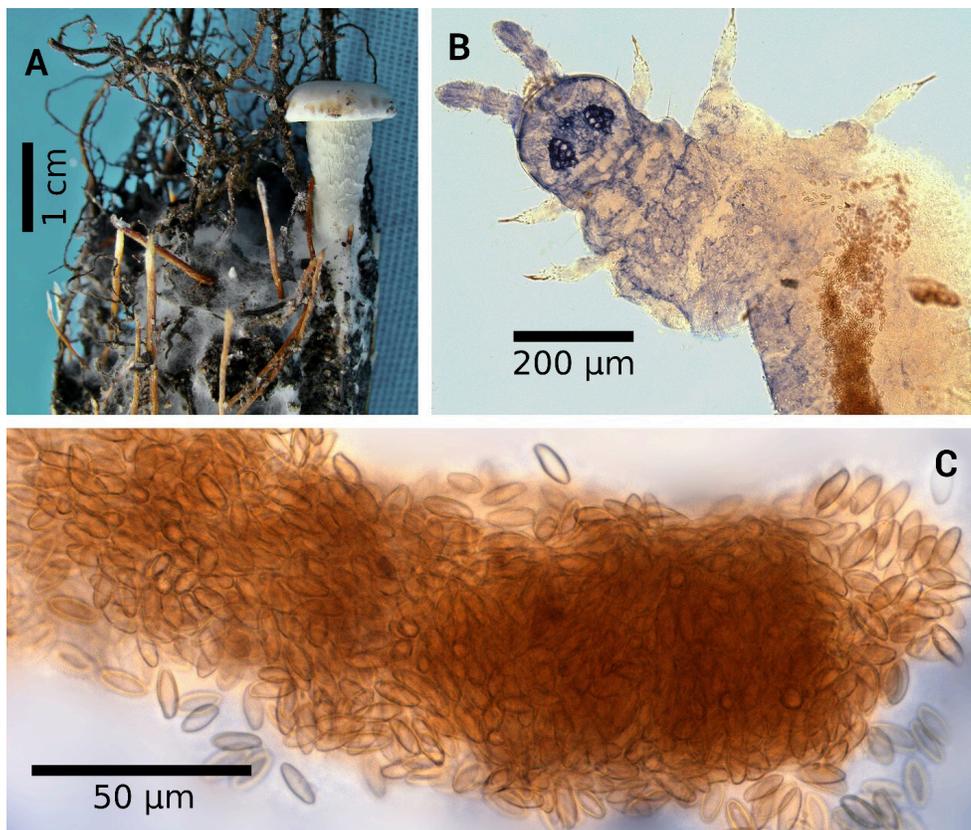
Figure 5. A: Sporome of *Hebeloma mesophaeum*. B: *Mitchellania* ca. *vulgaris* found dwelling on sporome of *H. mesophaeum*. C: Spores of *H. mesophaeum* in the digestive tract of *M.* ca. *vulgaris*.
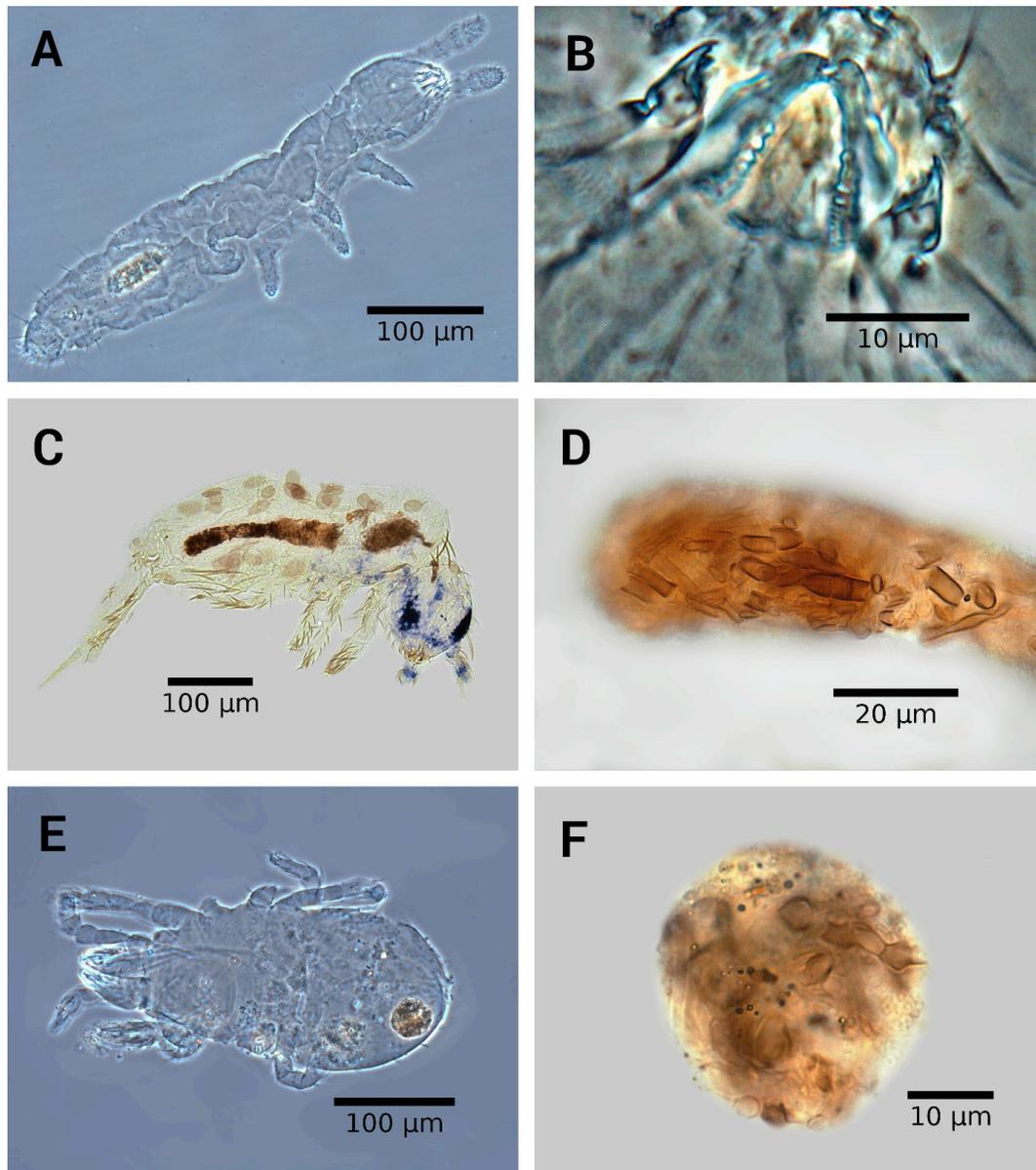
Figure 6. A: Soil and hyphae dwelling *Mesaphorura florae*. B: Chewing mouthparts of *M. florae* with very developed molar area in the jaws to triturate detritus and fungi. C: *Lepidocyrtus* sp. found dwelling on *Laccaria laccata*. D: Hyphae of *L. laccata* in the digestive tract of *Lepidocyrtus* sp. E: *Alicorhagia usitata* found dwelling on *Wilcoxina* sp. F: Hyphae of *Wilcoxina* sp. in the gut content of *A. usitata*.

In relation to the species of Acari, it was found that *Alicorhagia usitata* feeds on the hyphae of *Wilcoxina* sp. (Figure 6e and 6f). Walter *et al.* (1988) mentioned that Endeostigmata are important nematophages and that the species of Alicorhagiidae are best considered omnivores; when nematodes are not available, the adults feed on fungi. Contrary to what was reported by Schneider and Maraun (2005), a feeding preference for dark pigmented mycelium was not observed because we did not find evidences in the gut contents of the other species (excepting some individuals of *Mesaphorura*) that inhabited the mycelium of *Wilcoxina* sp. Finally, Walter *et al.* (1988) showed that *Protogamasellus mica* and mites of the genus *Asca* presented high rates of feeding preference for nematode and collembolans preys. The presence of *P. mica* in the mycelium of the three ectomycorrhizal fungi indicate its ecological role as population regulators of the collembolan populations on the ERM, which places predatory mites in a high trophic-level in the food web of the ERM of the ectomycorrhizal fungi.

CONCLUSIONS

The study of interactions between the mycelium of ectomycorrhizal fungi and soil mesofauna is important not only to understand the ERM functions, but also to have a broader insight of the nature of the relationships that drive and regulate ecosystem processes. Collembolans and mites dwelling the mycelium of ectomycorrhizal fungi are poorly known. We found that there was not difference in the abundance and community structure but there was an effect on species richness and species dominance of total number of mesofauna that was recorded. The dominance structure analysis helped to explain the interaction of the mesofauna with the ERM associated to *Pinus greggii* roots inoculated with ectomycorrhizal fungi. It was observed a food web in terms of functional groups that share the mycelial habitat being indicated for the feeding and habitat preferences of collembolans and mites, as a result of their life forms. Otherwise, mycelium is composed of a filamentous network of hyphae which might conforms diverse habitats for mesofauna depending of the filament elasticity, hyphae filament diameter, branching and network density as well as fruiting body formation. *Wilcoxina* sp. presents a high network density and branching that showed few soil mesofauna taxonomic groups dwelling the mycelium, expressed as a low species richness, compared to the less network density of the mycelium of *L. laccata* and *H. mesophaeum*. Properties of the mycelium result in the formation of trophic niches in relation to life forms of mesofauna shaping the food web on the ERM among the different ectomycorrhizal fungi studied and, therefore the mycelium might be an evolutionary force in structuring species composition, diversity, and stability of mesofauna communities.

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