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FULL PAPER

Soil factors influencing ectomycorrhizal sporome distribution in neotropical forests dominated by *Pinus montezumae*, Mexico

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Abstract Soil factors influencing ectomycorrhizal (ECM) sporome distribution in neotropical forests dominated by *Pinus montezumae* were examined at Sierra Chichinautzin, Mexico. Study sites were located on three volcanoes of different ages and ECM sporomes were collected during three consecutive years. *Inocybe* and *Laccaria* species were preferentially found at the youngest site, while *Tricholoma* and *Russula* species showed a more abundant distribution at the oldest site. Total sporome richness was negatively correlated with carbon (C) and nitrogen (N) contents in the soil organic horizon. Canonical correspondence analysis (CCA) was used to investigate the relationships between sporome species and soil variables. The CCA biplot showed that *Amanita rubescens*, *I. fastigiata*, and *I. geophylla* had a strong positive relationship with soil C and N contents, whereas *Inocybe* sp.4 was negatively related to these variables. This indicates an intra-generic variability in fungal responses to soil factors. The measured soil nutrients influenced species composition patterns, and the differences in sporome distribution evidenced a large degree of community specialization along the soil quality gradient. Together, these data contribute to a better understanding of the ecology of macrofungi in neotropical forests.

Keywords Ectomycorrhizal fungi · Soil quality · Macrofungi · *Inocybe* · Species richness

Introduction

Ectomycorrhizal (ECM) fungi provide soil resources to their tree hosts and receive carbohydrates in exchange (Göttlicher et al. 2008; Smith and Read 2008) and as such represent an interface between the soil and the host tree (Smits et al. 2008). ECM fungal communities can be assessed through sporome surveys or root tip sampling. Although some authors have considered sporomes as a poor measure of the mycorrhizal status of tree roots (Gardes and Bruns 1996; Richard et al. 2005; Smith et al. 2007), sporomes constitute practical indicators in the estimation of forest fungal biodiversity (Kranabetter et al. 2005; Tóth and Barta 2010) and of soil productivity (Kranabetter et al. 2009a). They can also provide information about fungal characteristics and distribution patterns (Peter et al. 2001a; Baptista et al. 2010). They typically present high species diversity (Richard et al. 2004), and their distribution is sensitive to soil quality (Trudell and Edmonds 2004) and to stand age and forest composition (Twieg et al. 2007; Rinaldi et al. 2008). Additionally, they can be accurately identified with proper taxonomic training and can be surveyed across large areas. ECM fruiting bodies were thus used in the present study as a measure of ECM fungal community composition to assess how soil factors influence species distribution.

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Although many ECM fungi produce conspicuous fruiting bodies (Nara et al. 2003), the species composition of forest macrofungal communities and the factors influencing their distribution are still not well understood (Trudell and Edmonds 2004), especially in tropical regions. Moreover, only a minority of studies has been conducted under natural undisturbed conditions (Erland and Taylor 2002). More information has been generated concerning the influence of soil nitrogen (N) content on ECM fungal communities, due to the increasing presence of anthropogenic N gradients. Both species richness and abundance are affected by an increase in N availability (Lilleskov et al. 2001; Avis et al. 2008), and sporome species composition changes as well, since "nitrophilic" taxa are favored over "nitrophobic" ones. The relationships between ECM fungal diversity and other soil nutrients have been less investigated, and vary according to the dominant host tree species (Toljander et al. 2006).

In this study, we examined the influence of soil development on the epigeous ECM macrofungi along a soil chronosequence supporting neotropical forests. The dominance of *Pinus montezumae* Lamb. var. *montezumae* in these stands created ideal conditions to minimize the effects of host tree species on the relationships between soil quality and ECM community composition. In a previous study (Reverchon et al. 2010a), we found that species composition of ECM fungal communities as a whole varied according to edaphic conditions. Therefore, we carried out an extensive macrofungi survey in order to analyze in more detail how some selected soil variables were influencing particular fungal species. The contrasts in soil development across the chronosequence generated differences in soil nutrient status and quality: while older sites present a richer and more developed soil profile, young soils are only formed by an organic surface horizon (Peña-Ramírez et al. 2009). Hence, we examined the influence of topsoil quality (total carbon and nitrogen contents, C:N ratio, available phosphorus) on the distribution of specific ECM sporomes. We also investigated the existing relationship between the richness of the ECM sporome community and these soil variables.

Materials and methods

Study area

The study sites have been described in detail elsewhere (Reverchon et al. 2010a, b). Briefly, the Sierra del Chichinautzin Volcanic Field is located at the southern margin of Mexico City. Three volcanoes with different eruption times and therefore contrasting soil development stages were selected within the protected area Corredor Biológico Chichinautzin: the young Chichinautzin volcano (1835 years BP), the middle-aged Guespalapa volcano (4200 years BP), and the old Pelado volcano (10000 years BP). Soil properties were analyzed extensively (Peña-Ramírez et al. 2009) and soil quality appeared to improve with soil development. This volcanic chronosequence therefore forms an ideal framework to investigate the influence of soil parameters on ECM macrofungi composition without the bias of host tree species, age, or macroclimate effects.

To establish the sampling plots, one site per volcano was selected in order to minimize the effect of other variables: these sites were located at the same altitude (3100 m) on slopes of less than 10° with a southern orientation, and were covered by natural mature pine forests dominated by *P. montezumae*. Since the volcanoes are closely spaced (less than 5 km), climatic conditions in the area are similar: average annual temperatures vary from 10 to 14°C according to elevation, and precipitation ranges from 1000 to 1200 mm per year. Rainfall patterns are strongly seasonal, with 80% occurring during the rainy season, between June and October. Five adult individuals of *P. montezumae* were selected at each site and located at the center of five sampling plots (10 × 10 m). These sampling plots were separated by transects of approximately 50 m. The selected trees were chosen as far as possible from other ECM trees in order to avoid any interactions with other ECM hosts, although the presence of some individuals belonging to *Abies religiosa*, *Alnus firmifolia,* and *Quercus laurina* (Peña-Ramírez, personal communication) should be acknowledged. Dendrochronological studies (Peña-Ramírez, unpublished) permitted us to select trees that were approximately 80 years old. The average tree diameter was 46 cm at the young site and 62 cm at both the middle-aged and old sites. Average tree heights were 15, 20, and 32 m at the young, intermediate, and old sites, respectively.

Sporome collection and soil sampling

Ectomycorrhizal epigeous sporomes were collected weekly within the plots during three whole consecutive rainy seasons (from June to October 2005 to 2007). No sampling was carried out from November to May because sporome fructification usually occurs during the rainy season in neotropical areas (Garibay-Orijel et al. 2009; Rodríguez-Ramírez and Moreno 2010). Sporomes found on the transects between the plots were also recorded. Hypogeous fungi were not considered in this study because the lack of existing information in Mexico for those species would have constituted a strong limitation for their taxonomic identification, and because of the soil disturbance that their sampling requires. Sporomes were identified based on morphological characteristics, both macroscopic and microscopic (Arora 1986), and fungal genera were determined as ECM following Molina et al. (1992) and Rinaldi et al. (2008). Fungal nomenclature was based on Index Fungorum (http://www.indexfungorum.org/Names/Names.asp). Voucher specimens were dried at 60°C for 2 days and placed in the Herbarium of the Laboratorio Microcosmos Bioedáfico, at the Instituto de Geología, UNAM (access nos. MCCECTC001–MCCECTC2000).

Soil samples were previously collected from a soil profile at each location to determine the general soil characteristics of each study site. The totality of the results is presented in Peña-Ramírez et al. (2009). Soil depth was 35 cm at the young site, with more than 80% of stones after 6 cm, 35.5 cm at the middle-aged site, and 200 cm at the old site. The two youngest soils were formed by Ah and AC horizons, whereas the old soil, which was more developed, was formed by Ah, AB, Bw, BC, and C horizons.

Additionally, during the first rainy season, four soil samples per plot were collected in the soil Ah horizon to establish precise relationships between ECM sporome distribution and topsoil main nutrient contents. Samples were dried and sieved, and total carbon and nitrogen contents were measured through a Perkin Elmer 2400 analyzer (Waltham, MA, USA). Available phosphorus concentrations were determined following the methods described in Bray and Kurtz (1945). These results are summarized in Table 1. Because we chose to focus on how the main soil nutrients shaped ECM sporome distribution at the three volcanic sites, other general soil properties such as pH or water availability were not characterized at each sampling point. However, these variables were measured for each soil profile. A gradient in pH and water availability exists across the soil chronosequence, the young site being drier and more acid than the old site. How this gradient may influence ECM community structure is further discussed in Reverchon et al. (2010a).

Statistical analyses

Differences in main soil nutrient contents between the three sites were assessed with a Kruskal–Wallis test after soil variables were found to be non-normally distributed. Post-hoc paired differences were evaluated with a Mann–Whitney *U*-test with a Bonferroni correction for multiple comparisons. Taxonomic distribution was first investigated across the soil chronosequence at the genus level in order to unravel general patterns of fungal community composition. Moreover, species-level analyses were used to examine in detail the existing relationships between soil variables and the distribution of ECM sporomes. Fungal genera responses to soil factors are seldom straightforward (Lilleskov et al. 2001; Dickie et al. 2002; Rosling et al. 2003) and the effect of nutrient concentrations on fungal distribution, in particular the N content, is known to vary among species, even within the same genus (Trudell and Edmonds 2004). A species-level analysis was therefore the approach chosen to reduce the bias of intra-generic variation. The relationships between soil and fungal variables were determined using ECM sporomes collected exclusively inside the plots, where soil data were registered. The relationships between total abundance and total richness of the ECM sporome community with the measured soil factors were evaluated with Bonferroni-corrected Spearman correlation tests. Canonical correspondence analysis (CCA) was conducted using the R software (Ihaka and Gentleman 1996) in order to visualize the relative distribution of sites and ECM fungal species, based on sporome abundance. Only dominant taxa occurring at two or more plots were included in the analysis. Equilibrium circles and goodness of fit were used to test the significance of the relationships between community data and environmental parameters.

Results

ECM sporome communities

A total of 2795 sporomes of 153 ECM species were recorded at the three sites during the three consecutive sampling years (Supplementary Table 1). The youngest

Table 1 Soil age, classification, and main nutrient contents of the Ah horizon at the three study sites (modified from Reverchon et al. 2010b)

	Chichinautzin	Guespalapa	Pelado
Soil age (years BP)	1835 ± 55	2835 ± 75–4690 ± 90	9620 ± 160–10900 ± 280
Soil classification (World Reference Base 2006)	Mollic Leptosol	Lepti-vitric Andosol	Eutrisilic Andosol
C ($kg{\cdot}m^{-2}$)[A]	7.68 ± 0.63^{a}	17.8 ± 1.13^{b}	15.4 ± 1.36^{b}
N ($kg{\cdot}m^{-2}$)[A]	0.42 ± 0.03^{a}	1.04 ± 0.05^{b}	0.89 ± 0.06^{b}
C:N[A]	17.7 ± 0.78^{a}	16.9 ± 0.31^{a}	16.8 ± 0.45^{a}
P ($g\ m^{-2}$)[A]	2.13 ± 0.37^{ab}	2.39 ± 0.29^{a}	1.38 ± 0.19^{b}

Four soil samples were collected per plot (5 plots per site) in the Ah soil horizon. Different letters after mean ± SE indicate significant differences (Mann–Whitney, $p < 0.0125$)

[A] Mean value per site

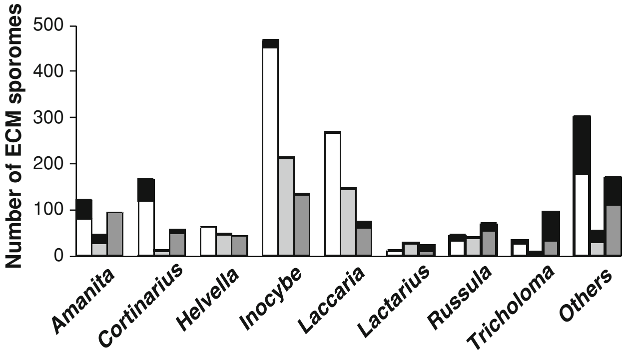

Fig. 1 Number of collected ectomycorrhizal (*ECM*) sporomes per genus and per site (*white* 1835 years BP, *light gray* 4200 years BP, *dark gray* 10,000 years BP). "Others" includes the fungal genera *Astraeus, Boletus, Cantharellus, Clavariadelphus, Clavulina, Entoloma, Gomphus, Gyrodon, Gyromitra, Gyroporus, Hebeloma, Hygrophorus, Leccinum, Leotia, Lyophyllum, Porphyrellus, Ramaria, Sarcodon*, and *Suillus*. *Black bars* represent the number of site-exclusive species

Table 2 Spearman correlation *R* values indicating the relationship between total abundance and richness of ectomycorrhizal sporome species and soil variables

	Soil C content (kg m^{-2})	Soil N content (kg m^{-2})	Soil C:N ratio	Soil P content (g m^{-2})
Total abundance	−0.491	−0.477	0.272	−0.107
Total richness	−0.734*	−0.670*	0.161	0.045

* Significant correlation at $p < 0.00625$

site presented the greatest ECM sporome abundance (1467 sporomes collected during three consecutive years, against 578 for the middle-aged site and 750 for the oldest site) and richness (109 ECM species against 69 for the middle-aged site and 78 for the oldest site).

When ECM sporome community composition was analyzed at the genus level, the three study sites appeared to be quite different (Fig. 1). *Inocybe* and *Laccaria* sporomes were abundantly recorded across the whole chronosequence, especially at the youngest site, and presented a relatively low proportion of site-exclusive species. On the other hand, *Cortinarius* and *Tricholoma* showed a more definite site-distribution and higher proportions of site-exclusive species (59 and 73%, respectively). The largest proportion of site-exclusive species was found at the youngest site (38.5%, against 27.5% for the middle-aged site and 23.1% for the old site).

Correlation and multivariate analyses

Spearman correlations were used to determine potential relationships between total abundance and richness of the ECM sporome community and the measured soil variables (Table 2). Species richness was significantly and negatively correlated with total C and N contents in the soil organic horizon, indicating that sporome richness was higher at the youngest, less fertile site (Fig. 2).

The ordination biplot of CCA analysis (Fig. 3) showed that the communities of ECM sporomes at the 15 sampling plots were not clearly segregated into groups corresponding to the three volcanoes. The first and second axes of the diagram explained 25 and 20% of the variation in fungal distribution, respectively. Soil C and N contents were the constraining variables with the highest score for the "*x*" axis (−0.83, −0.88, and 0.75 for soil C, N, and C:N, respectively). Species on the left of the biplot and with the highest scores, such as *Amanita rubescens* Pers., *Inocybe fastigiata* (Schaeff.) Quél., and *Inocybe geophylla* (Pers.) P. Kumm. have a positive relationship with topsoil C and N contents and a negative one with the C:N ratio of the soil organic horizon, and are therefore more abundant at the oldest site. Soil available P obtained the highest score for the "*y*" axis of the biplot (0.85), with species to the top, such as *Amanita* sp.1 and *Lactarius salmonicolor* R. Heim & Leclair, positively related to P content in the soil organic horizon and therefore associated with the young sites. The equilibrium circle determined that 11 fungal species contributed significantly to the ordination biplot: *A. rubescens*, *Amanita* sp.1, *I. fastigiata*, *I. geophylla*, *Inocybe* sp.1, sp.2, sp.4, sp.7, and sp.8, *Laccaria amethystina* Cooke, and *L. salmonicolor* (Supplementary Figure 1).

Analyzing the goodness of fit of these 11 fungal species, we found two different patterns. One group of species contributed significantly to the "C and N" axis, their goodness of fit value being larger for the "*x*" axis. This group was constituted by *A. rubescens, I. fastigiata*, *I. geophylla, Inocybe* sp.2, sp.4, and sp.7. The second group of species, formed by *Amanita* sp.1, *Inocybe* sp.1 and sp.8, and *L. amethystina*, presented larger values of goodness of fit for the "*y*" axis and were therefore strongly related to the soil P content. Only *L. salmonicolor* did not belong to either of these groups, its goodness of fit value being larger for a fourth axis of the CCA, constrained by both soil P and the C:N ratio.

Discussion

Total abundance and richness of the ECM sporome community were higher at the youngest, less fertile site. These findings coincide with Baar and ter Braak's (1996) ordination diagram, which suggested that small nutrient and organic matter contents were favourable to ECM fungi. Gehring et al. (1998) also reported that ECM fungal richness did not decrease with lower soil nutrient and moisture

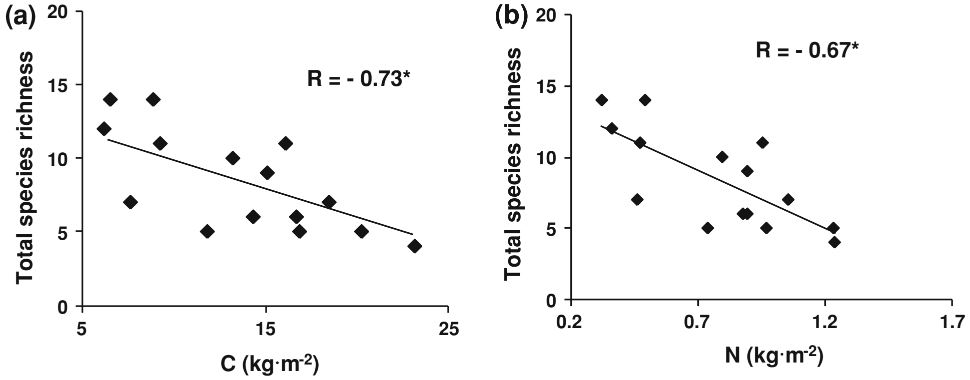

Fig. 2 Total species richness by sampling plot in correlation with **a** soil C content (kg m^{-2}) and **b** soil N content (kg m^{-2}). *R* represents the Spearman correlation coefficient (*Asterisk* indicates significance at $p < 0.00625$). *Each point* is a plot average across three sampling years

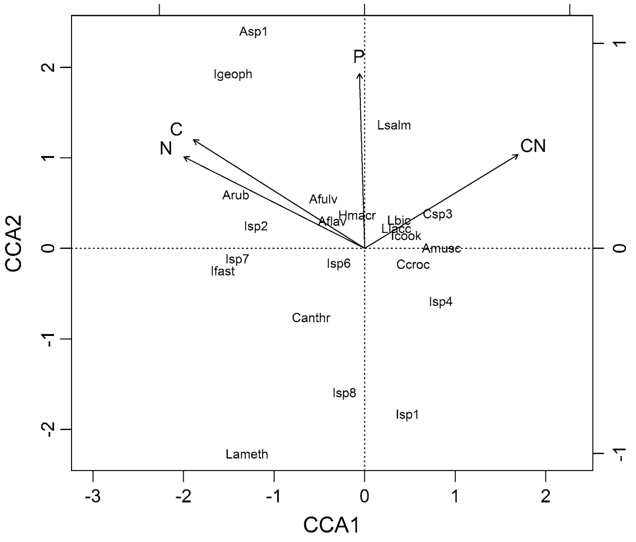

Fig. 3 Canonical correspondence analysis (*CCA*) ordination biplot of ECM sporome species associated with *Pinus montezumae* based on their abundance at the three study sites during three consecutive sampling years, constrained by soil factors. Aflav, *Amanita flavoconia* G.F.Atk; Afulv, *Amanita fulva* (Schaeff.) Fr.; Amusc, *Amanita muscaria* (L.) Lam.; Arub, *Amanita rubescens* Pers.; Asp1, *Amanita* sp.1; Canthr, *Cortinarius anthracinus* (Fr.) Fr.; Ccroc, *Cortinarius croceus* (Schaeff.) Gray; Csp3, *Cortinarius* sp.3; Hmacr, *Helvella macropus* (Pers.) P. Karst.; Icook, *Inocybe cookei* Bres.; Ifast, *Inocybe fastigiata* (Schaeff.) Quél.; Igeoph, *Inocybe aff. geophylla* (Pers.) P. Kumm.; Isp1, *Inocybe* sp.1; Isp2, *Inocybe* sp.2; Isp4, *Inocybe* sp.4; Isp6, *Inocybe* sp.6; Isp7, *Inocybe* sp.7; Isp8, *Inocybe* sp.8; Lameth, *Laccaria amethystina* Cooke; Lbic, *Laccaria bicolor* (Maire) P.D. Orton; Llacc, *Laccaria laccata* (Scop.) Cooke; Lsalm, *Lactarius salmonicolor* R. Heim & Leclair

levels, which is in agreement with our study, since richness was negatively correlated to both soil C and N contents. Many ECM fungi associated with pine species appear to present a negative relationship with soil fertility (Berch et al. 2006; Parrent et al. 2006; Taniguchi et al. 2007), whereas fungi associated with other conifers seem to require richer soils (Toljander et al. 2006; Kranabetter et al. 2009b). *Inocybe* sp.4 was negatively related to topsoil C and N contents, and species such as *Inocybe* sp.1, *Inocybe* sp.8, and *L. amethystina* were negatively related to soil available P. Species within the same fungal genus responded differently to the measured soil variables, which demonstrates the relevance of species-level analyses to study fungal responses to edaphic factors. *A. rubescens,* for instance, responded positively to total C and N contents in the soil organic horizon, whereas *Amanita* sp.1 obtained a very high score on the ordination biplot for its relationship with available P. Molecular data seem to indicate the similarity of *Amanita* sp.1 and *Amanita imazekii* reported by Oda et al. (2001), and further analyses are currently being carried out to determine the extent of this similarity. Various studies have highlighted the importance of P in shaping ECM community structure (Morris et al. 2008; Twieg et al. 2009). Twieg et al. (2009) also reported a negative relationship between soil available P and ECM fungal richness as a whole, but indicated that the abundance of specific taxa (in that case *Rhizopogon vinicolor* and *Cenococcum geophilum*) was positively related to P. The nutritional requirements of ECM fungi are likely to vary between species, some taxa being better adapted to grow on soils with higher available P content.

Nevertheless, it is difficult to compare our findings with other studies since the gradients in soil fertility they considered to influence species composition are often human-induced (Tarvainen et al. 2003; Rineau and Garbaye 2009). This is especially the case for studies on nitrogen gradients where N levels are much higher than those described here. Despite these discrepancies, we also found that N was negatively correlated with the species richness of ECM sporomes, which is in agreement with the findings of other authors (Jonsson et al. 2000; Lilleskov et al. 2001). On the contrary, the species richness of root tip communities at the three sites was not affected by N (Reverchon et al. 2010a). This concurs with the results of previous works which report a stronger effect of N on ECM aboveground communities (Jonsson et al. 2000; Peter et al. 2001b; Avis et al. 2003), possibly due to a reduction of resource allocation to sporomes under N-enriched conditions (Lilleskov and Bruns 2001). The species composition of ECM belowground communities is therefore more likely to be related to soil fertility than to total abundance or richness (Reverchon et al. 2010a).

Weekly surveys throughout entire sporome production seasons are necessary in order to obtain accurate information about fungal community structure, as suggested by Vogt et al. (1992) and Nara et al. (2003). In the present case, sampling during three consecutive whole rainy seasons showed that species composition was different across the soil chronosequence under study. Dominant genera at the youngest and middle-aged sites were *Laccaria* and *Inocybe*, whereas dominant ones at the oldest site were *Amanita* and *Tricholoma*. Multi-site species, such as *Inocybe cookei* Bres. and *Laccaria bicolor* (Maire) P.D. Orton, are useful biodiversity indicators, since they could contribute to the resiliency of forest ecosystems, as suggested by Kranabetter et al. (2009a). The differences in the distribution of ECM species determined in this study evidenced a high degree of community specialization along the soil quality gradient. The highest site-exclusiveness for ECM species was recorded at the youngest site, which is similar to what was previously reported for saprophytic fungi (Reverchon et al. 2010b), and was probably enhanced by the spatial heterogeneity and presence of edaphic microniches inherent to young volcanic soils. Site-exclusive species may be suited to particular soil conditions and thus may increase utilization of soil nutrients (Twieg et al. 2009). This may be particularly true at the youngest site where mature pine forests are able to establish despite soil limitations. The examination of ECM root tips from *P. montezumae* at the same study sites (Reverchon et al. 2010a) has shown that their greater abundance at the young site is crucial for water uptake, since the relatively small water-holding capacity and large evaporation rates at Chichinautzin are limiting factors for tree growth.

Neotropical forests and their associated mycobiota have been scarcely studied (Liang et al. 2007) and the majority of the works carried out in these regions have focused on edible mushrooms only, since mushroom-picking is an activity of primordial social and economic importance in Mexico (Zamora-Martínez and Nieto de Pascual-Pola 1995; Garibay-Orijel et al. 2006; Pérez-Moreno et al. 2008; Garibay-Orijel et al. 2009). The determination of fungal species in tropical countries is limited by the fact that many identification keys are made for European or North-American macrofungi, which explains why several taxa could not be identified at the species level. Some of them may even correspond to new, still undescribed, fungal species. This study therefore represents a significant contribution toward a better understanding of the diversity and ecology of macrofungi in neotropical forests.

The species composition of ECM sporome communities is a key factor for the analysis of the ecological functions of these fungi, since ECM species reproduction is carried out through fruiting bodies. Sporomes are therefore a relevant indicator of ECM community structure, although it is important to acknowledge that they constitute only a partial assessment of ECM fungal communities. While previous works have focused on stand age chronosequences to examine the subsequent changes in fungal communities, further research analyzing the detailed relationships between soil quality and ECM fungal species will be necessary to generate more information about the dynamics of species distribution in different edaphic conditions. A number of other site properties, such as soil moisture, pH, and temperature, or N and P mineralization rates, may also influence ECM species composition and would need to be included in the multivariate analysis, for a better understanding of the influence of soil and soil processes on the occurrence of ECM sporomes.

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References

Arora D (1986) Mushrooms demystified, 2nd edn. Ten Speed Press, Berkeley

Avis PG, McLaughlin DJ, Dentinger BC, Reich PB (2003) Long-term increase in nitrogen supply alters above- and below-ground ectomycorrhizal communities and increases the dominance of *Russula* spp. in a temperate oak savanna. New Phytol 160:239–253

Avis PG, Mueller GM, Lussenhop J (2008) Ectomycorrhizal fungal communities in two North American oak forests respond to nitrogen addition. New Phytol 179:472–483

Baar J, ter Braak CJF (1996) Ectomycorrhizal sporome occurrence as affected by manipulation of litter and humus layers in Scots pine stands of different age. Appl Soil Ecol 4:61–73

Baptista P, Martins A, Tavares RM, Lino-Neto T (2010) Diversity and fruiting pattern of macrofungi associated with chestnut (*Castanea sativa*) in the Trás-os-Montes region (Northeast Portugal). Fungal Ecol 3:9–19

Berch SM, Brockley RP, Battigelli JP, Hagerman S, Holl B (2006) Impacts of repeated fertilization on components of the soil biota under a young lodgepole pine stand in the interior of British Columbia. Can J For Res 36:1415–1426

Bray RH, Kurtz LT (1945) Determination of total, organic, and available forms of phosphorus in soils. Soil Sci 59:39–45

Dickie IA, Xu B, Koide RT (2002) Vertical niche differentiation of ectomycorrhizal hyphae in soil as shown by T-RFLP analysis. New Phytol 156:527–535

Erland S, Taylor AFS (2002) Diversity of ecto-mycorrhizal fungal communities in relation to the abiotic environment. In: van der Heijden MGA, Sanders IR (eds) Mycorrhizal ecology. Ecological studies. Springer, Berlin, pp 163–200

Gardes M, Bruns TD (1996) Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: above- and below-ground views. Can J Bot 74:1572–1583

Garibay-Orijel R, Cifuentes J, Estrada-Torres A, Caballero J (2006) People using macro-fungal diversity in Oaxaca, Mexico. Fungal Divers 21:41–67

Garibay-Orijel R, Córdoba J, Cifuentes J, Valenzuela R, Estrada-Torres A, Kong A (2009) Integrating wild mushrooms use into a model of sustainable management for indigenous community forests. For Ecol Manag 258:122–131

Gehring CA, Theimer TC, Whitham TG, Keim P (1998) Ectomycorrhizal fungal community structure of pinyon pines growing in two environmental extremes. Ecology 79:1562–1572

Göttlicher SG, Taylor AFS, Grip H, Betson NR, Valinger E, Högberg MN, Högberg P (2008) The lateral spread of tree root systems in boreal forests: estimates based on ^{15}N uptake and distribution of sporocarps of ectomycorrhizal fungi. For Ecol Manag 255:75–81

Ihaka R, Gentleman R (1996) R: a language for data analysis and graphics. J Comput Graph Stat 5:299–314

Jonsson L, Dahlberg A, Brandrud TE (2000) Spatiotemporal distribution of an ectomycorrhizal community in an oligotrophic Swedish *Picea abies* forest subjected to experimental nitrogen addition: above- and below-ground views. For Ecol Manag 132:143–156

Kranabetter JM, Frieser J, Gamiet S, Kroeger P (2005) Ectomycorrhizal mushroom distribution by stand age in western hemlock—lodgepole pine forests of northwestern British Columbia. Can J For Res 35:1527–1539

Kranabetter JM, Frieser J, Gamiet S, Kroeger P (2009a) Epigeous fruiting bodies of ectomycorrhizal fungi as indicators of soil fertility and associated nitrogen status of boreal forests. Mycorrhiza 19:535–548

Kranabetter JM, Durall DM, MacKenzie WH (2009b) Diversity and species distribution of ectomycorrhizal fungi along productivity gradients of a southern boreal forest. Mycorrhiza 19:99–111

Liang Y, Guo LD, Du XJ, Ma KP (2007) Spatial structure and diversity of woody plants and ectomycorrhizal fungus sporomes in a natural subtropical forest. Mycorrhiza 17:271–278

Lilleskov EA, Bruns TD (2001) Nitrogen and ectomycorrhizal fungal communities: what we know, what we need to know. New Phytol 149:156–158

Lilleskov EA, Fahey TJ, Lovett GM (2001) Ectomycorrhizal fungal aboveground community change over an atmospheric nitrogen deposition gradient. Ecol Appl 11:397–410

Molina R, Massicotte H, Trappe JM (1992) Specificity phenomena in mycorrhizal symbiosis: community-ecological consequences and practical implications. In: Allen MF (ed) Mycorrhizal functioning: an integrative plant-fungal process. Chapman and Hall, London, pp 357–423

Morris MH, Smith ME, Rizzo DM, Rejmanek M, Bledsoe CS (2008) Contrasting ectomycorrhizal fungal communities on the roots of co-occurring oaks (*Quercus* spp.) in a California woodland. New Phytol 178:167–176

Nara K, Nakaya H, Hogetsu T (2003) Ectomycorrhizal sporocarp succession and production during early primary succession on Mount Fuji. New Phytol 158:193–206

Oda T, Tanaka C, Tsuda M (2001) *Amanita imazekii*—a new species in Amanita section Caesareae. Mycologia 93:1231–1234

Parrent JL, Morris WF, Vilgalys R (2006) CO_2-enrichment and nutrient availability alter ectomycorrhizal fungal communities. Ecology 87:2278–2287

Peña-Ramírez VM, Vázquez-Selem L, Siebe C (2009) Soil organic carbon stocks and forest productivity in volcanic ash soils of different age (1835–30,500 years B.P.) in Mexico. Geoderma 149:224–234

Pérez-Moreno J, Martínez-Reyes M, Yescas-Pérez A, Delgado-Alvarado A, Xoconostle-Cázares B (2008) Wild mushroom markets in Central Mexico and a case study at Ozumba. Econ Bot 62:425–436

Peter M, Ayer F, Egli S, Honegger R (2001a) Above- and below-ground community structure of ectomycorrhizal fungi in three Norway spruce (*Picea abies*) stands in Switzerland. Can J Bot 79:1134–1151

Peter M, Ayer F, Egli S (2001b) Nitrogen addition in a Norway spruce stand altered macromycete sporocarp production and below-ground ectomycorrhizal species composition. New Phytol 149:311–325

Reverchon F, Ortega-Larrocea MP, Pérez-Moreno J, Peña-Ramírez VM, Siebe C (2010a) Changes in community structure of ectomycorrhizal fungi associated to *Pinus montezumae* across a volcanic soil chronosequence at Sierra Chichinautzin, Mexico. Can J For Res 40:1165–1174

Reverchon F, Ortega-Larrocea MP, Pérez-Moreno J (2010b) Saprophytic fungal communities change in diversity and species composition across a volcanic soil chronosequence at Sierra del Chichinautzin, Mexico. Ann Microbiol 60:217–226

Richard F, Moreau PA, Selosse MA, Gardes M (2004) Diversity and fruiting patterns of ectomycorrhizal and saprobic fungi in an old-growth Mediterranean forest dominated by *Quercus ilex* L. Can J Bot 82:1711–1729

Richard F, Millot S, Gardes M, Selosse MA (2005) Diversity and specificity of ectomycorrhizal fungi retrieved from an old-growth Mediterranean forest dominated by *Quercus ilex*. New Phytol 166:1011–1023

Rinaldi AC, Comandini O, Kuyper TW (2008) Ectomycorrhizal fungal diversity: separating the wheat from the chaff. Fungal Divers 33:1–45

Rineau F, Garbaye J (2009) Effects of liming on ectomycorrhizal community structure in relation to soil horizons and tree hosts. Fungal Ecol 2:103–109

Rodríguez-Ramírez EC, Moreno CE (2010) Bolete diversity in two relict forests of the Mexican beech (*Fagus grandifolia* var. *mexicana*; Fagaceae). Am J Bot 97(5):893–898

Rosling A, Landeweert R, Lindahl BD, Larsson KH, Kuyper TW, Taylor AFS, Finlay RD (2003) Vertical distribution of ectomycorrhizal fungal taxa in a podzol soil profile. New Phytol 159:775–783

Smith SE, Read DJ (2008) Mycorrhizal symbiosis, 3rd edn. Academic Press, London

Smith ME, Douhan GW, Rizzo DM (2007) Ectomycorrhizal community structure in a xeric *Quercus* woodland based on rDNA sequence analysis of sporocarps and pooled roots. New Phytol 174:847–863

Smits MM, Bonneville S, Haward S, Leake JR (2008) Ectomycorrhizal weathering, a matter of scale? Mineral Mag 72:131–134

Taniguchi T, Kanzaki N, Tamai S, Yamanaka N, Futai K (2007) Does ectomycorrhizal fungal community structure vary along a Japanese black pine (*Pinus thunbergii*) to black locust (*Robinia pseudoacacia*) gradient? New Phytol 173:322–334

Tarvainen O, Markkola AM, Strömmer R (2003) Diversity of macrofungi and plants in Scots pine forests along an urban pollution gradient. Basic Appl Ecol 4:547–556

Toljander JF, Eberhardt U, Toljander YK, Paul LR, Taylor AFS (2006) Species composition of an ectomycorrhizal fungal community along a local nutrient gradient in a boreal forest. New Phytol 170:873–884

Tóth BB, Barta Z (2010) Ecological studies of mycorrhizal fungi: an analysis of survey methods. Fungal Divers 45:3–19

Trudell SA, Edmonds RL (2004) Macrofungus communities correlate with moisture and nitrogen abundance in two old-growth conifer forests, Olympic National Park, Washington, USA. Can J Bot 82:781–800

Twieg BD, Durall DM, Simard SW (2007) Ectomycorrhizal fungal succession in mixed temperate forests. New Phytol 176:437–447

Twieg BD, Durall DM, Simard SW, Jones MD (2009) Influence of soil nutrients on ectomycorrhizal communities in a chronosequence of mixed temperate forests. Mycorrhiza 19:305–316

Vogt KA, Bloomfield J, Ammirati JF, Ammirati SR (1992) Sporocarp production by basidiomycetes, with emphasis on forest ecosystems. In: Carroll GC, Wicklow DT (eds) The fungal community: its organization and role in the ecosystem, 2nd edn. Marcel Dekker, New York, pp 563–581

World Reference Base (2006) World reference base for soil resources, 2nd edn. World Soil Resources reports no. 103. FAO, Rome

Zamora-Martínez MC, Nieto de Pascual-Pola C (1995) Natural production of wild edible mushrooms in the southwestern rural territory of Mexico City, Mexico. For Ecol Manag 72:13–20