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ORIGINAL ARTICLE

Saprophytic fungal communities change in diversity and species composition across a volcanic soil chronosequence at Sierra del Chichinautzin, Mexico

Frédérique Reverchon · Pilar María del Ortega-Larrocea · Jesús Pérez-Moreno

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Abstract Saprophytic fungi are one of the most active decomposers of forest litter, and their diversity may be influenced by the spatial heterogeneity of substrates. We examined the changes in saprophytic community structure and composition across a volcanic soil chronosequence, at Sierra del Chichinautzin, Mexico. Saprophytic fungi were collected for three consecutive years at three sampling sites with contrasting soil properties in a volcanic soil chronosequence ranging from 1,835 years B.P. to 10,000 years B.P. Although no significant differences were found in terms of abundance and richness between the three sites, Shannon diversity was higher at the youngest, less-fertile site. The high percentage of site-exclusive species showed that species composition was strongly dependent on the site and therefore on soil parameters. Different saprophytic species had divergent responses to soil variables, but most fungal taxa correlated negatively with the edaphic factors we measured. The highest diversity found at the young, less fertile site may represent an "insurance" mechanism against harsh conditions, since different species are likely to play various ecological functions which may lead to a more efficient degradation of recalcitrant substrates.

Keywords Saprophytic fungi · Volcanic soil chronosequence · Fungal diversity · Community structure

F. Reverchon · P. María del Ortega-Larrocea
Instituto de Geología, Universidad Nacional Autónoma de México (UNAM),
04510 México, DF, México

J. Pérez-Moreno
Microbiología, Edafología, Colegio de Posgraduados,
Campus Montecillo, Km36.5 Carretera México-Texcoco,
56230 Montecillo, México

F. Reverchon (✉)
Departamento de Edafología, Instituto de Geología,
Universidad Nacional Autónoma de México (UNAM),
Apartado Postal 70-296,
04511 México, DF, México
e-mail: frederique_reverchon@hotmail.com

Introduction

Saprophytic fungi are one of the most active decomposers of forest litter and therefore play an important role in the cycling of carbon, nitrogen, and other soil nutrients (Smith and Read 2008). Basidiomycetes are reported to be especially important for organic matter decomposition as they produce a wide range of ligninocellulolytic enzymes (Dix and Webster 1995). Although most substrates can be decomposed by many fungal species, the decomposition ability of each species varies depending on environmental conditions (Deacon 1985; Schimel et al. 1999) and on interactions with other fungi (Robinson et al. 1993; Kuyper and Verschoor 1995). It is acknowledged that the presence of specific taxa depends on the type and quality of litter available (Steffen et al. 2000), although scarce information has been provided about the association of particular saprophytic species with particular types of soil.

Species composition of saprophytic fungal communities could determine the extent of organic matter decomposition, since different fungal species perform different ecological functions (Setälä and McLean 2004; Deacon et al. 2006) and occupy complementary niches (Hedger 1985). Different microhabitats or substrates could influence, in turn, the diversity of decomposer fungi (Lodge and Cantrell 1995; Laessøe et al. 1996), especially since soil nutrients are often patchily distributed (Boddy et al. 2009). This patchy distribution is particularly critical in volcanic soils

presenting a high spatial heterogeneity (Aplet et al. 1997). The discontinuous cover of young volcanic soils by lava flows creates a large amount of microniches, which in turn could enhance fungal diversity (Lodge 1997; Sulkava and Huhta 1998).

Owing to the lack of mutualistic interaction with higher plants, saprophytes are expected to be more dependent upon their respective substrates than are mycorrhizal fungi (Gebauer and Taylor 1999) and could therefore be influenced by abiotic factors such as soil nutrients or soil moisture (Zakaria and Boddy 2002; Richard et al. 2004). In order to examine the effect of soil factors on saprophyte fungal communities, we assessed the abundance, richness and diversity patterns of those communities across a volcanic soil chronosequence, where the different stages of pedogenesis generated contrasting soil properties. As soil develops, its nutrient status changes and soil quality as a whole improves (Peña-Ramírez et al. 2009). Since the mycelium of these fungi typically extend at the soil-litter interface (Boddy et al. 2009), these changes could influence the structure and species composition of the saprophytic fungal communities.

Methods

Study sites

This study was carried out at the Sierra del Chichinautzin Volcanic Field, located in the Trans-Mexican Volcanic Belt, at the southern margin of the Mexico City area. The Sierra is composed of numerous monogenetic volcanoes of different ages (Márquez et al. 1999), forming a chronosequence of volcanic soils. Three volcanoes of contrasting ages were selected: the young Chichinautzin volcano (1,835 years B.P.), the middle-aged Guespalapa volcano (4,200 years B.P.) and the oldest Pelado volcano (10,000 years B.P.). These volcanoes are closely spaced (less than 5 km) and are part of the Sierra del Chichinautzin Protected Area (Corredor Biológico de la Sierra del Chichinautzin). At each volcano, a study site was chosen. These study sites and their characteristics have been extensively described (see Peña-Ramírez et al. 2009). Volcanic soils at these sites present different stages of pedogenesis and therefore contrasting soil qualities (Table 1). Other site characteristics were kept similar in order to examine exclusively the influence of soil parameters: the altitude at the three sites was 3,100 m.a.s.l. and the slopes were less than 10° with southern orientation. Rainfall in the region shows a marked seasonality (80% of rains occur during the rainy season, between June and October). The dominant vegetation in the area is a pine–oak natural forest (Velázquez 1994) and the tree community at the three study sites is dominated by mature individuals of *Pinus montezumae* Lamb. var. *montezumae*. Four soil samples were taken in the soil organic horizon at the cardinal points of each plot in order to establish precise relationships between sporocarp distribution and soil properties. Soil sampling was performed in the first year of survey, through 2.5-cm-diameter×20-cm-length soil cores. However, since soil depth at the youngest site did not reach 6 cm, 5×5 cm cores were used for sampling in order to obtain the same soil volume. All the soil samples were dried and sieved (<2 mm). Plant available phosphorus (P) concentration was determined in each sample (Bray and Kurtz 1945); total nitrogen (N) and carbon (C) analyses were performed with a Perkin Elmer 2400 analyser. Relevant site characteristics and properties of the soil organic horizon at each study sites are presented in Table 1.

Sampling of saprophytic sporocarps

Five plots (10×10 m) were established at each site in order to sample saprophytic sporocarps. These plots were separated from each other by approximately 100 m. Sporocarps were collected weekly on forest litter and decaying logs inside the plots and along transects between them during three consecutive rainy seasons (2005–2007), these transects varying from 30 to 70 m. We used both macroscopic and microscopic characteristics for sporocarp identification (Bon 2004). Abundance and species richness were measured at each site. Voucher specimens were dried and stored in the Herbarium of the Laboratorio Microcosmos Bioedáfico, at the Instituto de Geología, UNAM.

Diversity assessment and statistical analysis

We examined differences in sporocarp abundance and richness between sites using one-way ANOVA and Mann-Whitney *U* tests. The analyses were based on the abundance and richness patterns of saprophytic communities in the five plots established at each site. Species composition of fungal communities was assessed through rank-abundance curves of the dominant saprophytic species at each site. We defined as abundant species with a relative abundance higher than 1%. Shannon diversity index was used to evaluate and compare the diversity of saprophytic sporocarp communities across the soil chronosequence. Canonical correspondence analysis (CCA) was used to assess the relationships between dominant fungal species and soil factors at the site level. An equilibrium circle was used on the ordination plot to determine whether fungal genera significantly influenced the overall fungal distribution. The patterns revealed by CCA were thereafter tested for significance by Spearman correlation analysis. Due to practical limitations, soil variables were measured during the first sampling year only. Therefore, CCA and correlation analysis were performed with the 2005 sporocarp data

Table 1 General site characteristics (modified from Peña-Ramírez et al. 2009) and selected soil variables of the plots surveyed for saprophytic sporocarps at the three study sites

	Young site					Middle-aged site					Old site				
Age of land surface (years B.P.[a])	1,835±55					2,835±75 to 4,690±90					9,620±160 to 10,900±280				
UTM Coordinates	X: 482,041, Y: 2,109,907					X: 482,037, Y: 2,109,903					X: 475,922, Y: 2,114,796				
Soil classification (WRB 2006)	Mollic Leptosol					Lepti-vitric Andosol					Eutrisilic Andosol				
Total soil depth (cm)	6–35					30–41					193–200				
Available water (L m^{-2})	28.2					95.4					301.6				
Soil organic horizon depth (cm)	5					27					43				
Soil organic horizon properties by plot	P1	P2	P3	P4	P5	P1	P2	P3	P4	P5	P1	P2	P3	P4	P5
C (kg m^{-2})	8.9	6.2	7.6	6.5	9.2	16.1	20.2	14.3	15.1	23.1	16.7	13.2	18.5	11.8	16.8
Mean per site[b]	7.68±0.63 a					17.8±1.13 b					15.4±1.36 b				
N (kg m^{-2})	0.49	0.36	0.46	0.32	0.47	0.96	1.23	0.87	0.89	1.24	0.89	0.8	1.06	0.74	0.97
Mean per site[b]	0.42±0.03 a					1.04±0.05 b					0.89±0.06 b				
C:N	18.4	17.2	17.5	18.3	17.3	16.6	16.4	16.2	16.8	18.5	18.3	16.4	17.3	15.1	17
Mean per site[b]	17.7±0.78 a					16.9±0.31 a					16.8±0.45 a				
P (g m^{-2})	1.76	0.59	3.48	1.49	3.35	2.55	1.14	2	2.59	3.65	1.16	1.31	2.45	0.69	1.28
Mean per site[b]	2.13±0.37 ab					2.39±0.29 a					1.38±0.19 b				

[a] *B.P.* Before Present. Last eruption date and start of soil formation. The dates correspond to non-calibrated ^{14}C dates (Siebe et al. 2004)

[b] Different letters in columns indicate significant differences (Mann-Whitney *U* Test, $p<0.05$)

exclusively, since soil factors at such a small scale are likely to vary from one year to another. Statistical analyses were conducted using the R software (http://www.r-project.org) (Ihaka and Gentleman 1996).

Results

A total of 1,331 specimens were collected during the 3 years of sampling and 72 saprophytic species were identified (Table 2). From these 72 species, 38 were found at the youngest site, 29 at the middle-aged site and 37 at the oldest site of the soil chronosequence. All but three species were Basidiomycetes. Most of the collected species were litter decomposers, although some woody-debris saprotrophs were collected from the forest floor. These belong to the genera *Cyathus*, *Gymnopilus*, *Hypholoma*, *Pholiota* and *Pluteus*.

Of particular importance was the case of *Auriscalpium vulgare* Gray which grows specifically on pine cones and needles. This species was found to be present at all three sites, as expected given the predominance of pine species in the tree community, and to fruit abundantly at the old site. A total of 158 specimens of *A. vulgare* were collected at the old site during the three sampling years, against 5 at the young site and 19 at the middle-aged site. *Auriscalpium vulgare* is known to be widely distributed in Europe and Asia, as well as in North and Central America (Petersen and Cifuentes 1994). Because of its substrate specificity and lack of interaction with the soil organic horizon (Bon 2004), we did not consider this species in the present analysis.

No significant differences were found in either abundance or richness between the saprophytic sporocarp communities, although more specimens were collected at the middle-aged site, where 489 sporocarps were sampled, against 416 at the young site and 427 at the old site (Table 3). However, Shannon diversity index results were different between the study sites, being significantly lower at the middle-aged site and higher at the youngest site. Since the Shannon index considers both richness and species relative abundance, it is important to examine more precisely the differences between saprophytic communities at the three sites in terms of species composition.

Site-exclusive species (species found exclusively at one site) were the most abundant and represented 67% of total richness, whereas 16 species (22%) were shared by two sites and only 8 species (11%) were common to all three sites. Site-exclusiveness was especially important at Chichinautzin as half the saprophytic species were only found at the youngest site. These belonged to the fungal genera *Galerina*, *Hygrocybe* and *Mycena*, whereas species such as *Cyathus olla* (Batsch) Pers. and *Cyathus striatus* (Huds.) Willd. were exclusive to the middle-aged site and *Marasmius*

Table 2 Saprophyte sporocarp species, sampled during three consecutive rainy seasons at the three study sites

	Young site			Middle-aged site			Old site		
	2005	2006	2007	2005	2006	2007	2005	2006	2007
Agaricus sp.[a]			1						
Agrocybe sp.[a]								1	
Clitocybe aff. *costata* Kühner & Romagn.[a]		1							
Clitocybe aff. *dealbata* (Sowerby) Gillet[a]				4					
Clitocybe gibba (Pers.) P. Kumm.	2	3	16	14	4	5	2	1	
Clitocybe aff. *squamulosa* (Pers.) Fr.	1								1
Clitocybe sp.	2		13		1				
Collybia sp.	6			5	1		5	4	6
Coprinopsis atramentaria (Bull.) Readhead, Vilgalys & Moncalvo[a]								1	
Coprinus comatus (O.F. Müll.) Pers.					3	1		8	
Coprinus aff. *cortinatus* J.E. Lange[a]							4		
Coprinus sp.				4	2			12	
Cyathus olla (Batsch) Pers.[a]				10	58				
Cyathus striatus (Huds.) Willd.[a]				100					
Galerina aff. *hypnorum* (Schrank) Kühner[a]	5	38	30						
Geoglossum cookeanum Nannf.[a]	2								
Gymnopilus penetrans (Fr.) Murrill					13			2	
Gymnopilus aff. *spadiceus* Romagn.[a]	4								
Gymnopilus sp.			1						2
Gymnopus acervatus (Fr.) Murrill[a]		3							
Gymnopus aff. *confluens* (Pers.) Antonín, Halling & Noordel.[a]								2	
Gymnopus dryophilus (Bull.) Murrill	5	5	14	5	3	1	16	43	28
Gymnopus erythropus (Pers.) Antonín, Halling & Noordel.[a]		1							
Gymnopus aff. *fusipes* (Bull.) Gray						2		5	
Gymnopus aff. *peronatus* (Bolton) Antonín, Halling & Noordel.[a]							2		
Gymnopus aff. *perforans* (Hoffm.) Antonín & Noordel[a]									4
Hygrocybe miniata (Fr.) P. Kumm.[a]		1	10						
Hygrocybe persistens var. *konradii* (R. Haller Aar.) Boertm.[a]	1								
Hygrocybe sp.	12	3	6	6			12	4	
Hygrophoropsis aurantiaca (Wulfen) Maire	1			3	10		99	25	18
Hypholoma fasciculare var. *fasciculare* (Huds.) P. Kumm.		3	5	10	80	74	17	10	10
Hypholoma sp.				1			12		
Lepiota sp.	7				1	9	1	8	19
Lepista flaccida (Sowerby) Pat.[a]					3				
Lycoperdon mammiforme Pers.	5	5	6	7	4	6			
Lycoperdon perlatum Pers.	3	4	2			3			
Lycoperdon pyriforme Schaeff.[a]	5								
Lycoperdon umbrinum Pers.[a]							1		
Marasmius aff. *alliaceus* (Jacq.) Fr.[a]					1	1			
Marasmius aff. *androsaceus* (L.) Fr.[a]								6	
Marasmius oreades (Bolton) Fr.[a]							2	6	
Marasmius sp.		2			2	1		1	
Micromphale aff. *brassicolens* var. *brassicolens* (Romagn.) P.D. Orton[a]	11								
Mycena aff. *epipterygia* (Scop.) Gray[a]								3	1
Mycena aff. *filopes* (Bull.) P. Kumm.		3	2					1	5
Mycena aff. *galericulata* (Scop.) Gray[a]								2	

Table 2 (continued)

	Young site			Middle-aged site			Old site		
	2005	2006	2007	2005	2006	2007	2005	2006	2007
Mycena aff. *maculata* P. Karst.[a]								7	
Mycena aff. *metata* (Secr. ex Fr.) P. Kumm.[a]	2								
Mycena aff. *pura* (Pers.) P. Kumm.		1	1				4		
Mycena sp.1					5	2	2		
Mycena sp.2		1					3		
Mycena sp.3[a]	12	10							
Mycena sp.4[a]	4								
Mycena sp.5[a]							1		
Mycena sp.6				1			1		
Mycena sp.7[a]				2					
Mycena sp.8[a]		2							
Mycena sp.9[a]		49	2						
Mycena sp.10[a]					4				
Panaeolus sp.[a]		1							
Peziza sp.[a]		1							
Pholiota cerifera P. Karst.[a]				9					
Pholiota sp.[a]							3		
Pluteus cervinus (Schaeff.) P. Kumm.[a]								1	
Pluteus sp.[a]									1
Psathyrella sp.[a]				3					
Ramaria stricta (Pers.) Quél.[a]							2		
Rhodocollybia aff. *butyracea* (Bull.) Lennox			3			3			
Stropharia sp.[a]			3						
Trichoglossum hirsutum var. hirsutum (Pers.) Boud.[a]	17	30	15						
Tricholomopsis rutilans (Schaeff.) Singer[a]		2							
Tricholomopsis sp.[a]				1					

Numbers represent the number of sporocarp specimens collected at each study site, each year, for each saprophytic species

[a] Site-exclusive species

androsaceus (L.) Fr., *Marasmius oreades* (Bolton) Fr. or *Pluteus* spp. were only collected at the old site.

The discrepancy between species composition at the three study sites may be observed by examining the abundance of the main saprophytic fungal genera (Fig. 1). The young site was dominated by *Galerina* spp. and *Mycena* spp., whereas *Cyathus* spp. and *Hypholoma* spp. were the most abundant at the middle-aged site, and *Gymnopus* spp. and *Hygrophoropsis* spp. dominated at the old site.

Dominant species were defined as those with a relative abundance above 1%. Relative abundance curves of dominant species at each site showed that the number of dominant species was higher at the young site (17 dominant species at Chichinautzin against 14 at both Guespalapa and Pelado), generating stronger dominance patterns at the two oldest sites of the volcanic soil chronosequence (Fig. 2b and c). At the middle-aged site, *Hypholoma fasciculare* (Huds.) P. Kumm. was the most dominant species and represented 34% of total abundance, whereas *Hygrophoropsis aurantiaca* (Wulfen) Maire represented 33% of total abundance of saprophytic species at the oldest site. In contrast, the first dominant species only represented 18% at the youngest site (*Galerina hypnorum* (Schrank) Kühner; Fig. 2a). The first three dominant species represented 68% at the middle-aged site, against 45% at the youngest site and 62% at the oldest site. Only four of the dominant saprophytic species were common to the three sites of the chronosequence: *Collybia* sp., *Gymnopus dryophilus* (Bull.) Murrill, *Hygrocybe* sp. and *Hypholoma fasciculare* (Fig. 2).

The results of CCA ordination provided further insights into the effects of soil variables on the saprophytic sporocarp community at Sierra del Chichinautzin (Fig. 3). The first and second axis of the biplot explain 47.3 and

Table 3 Annual abundance, richness and diversity of the community of saprophyte sporocarps at the three sites

Sites	Abundance (number of specimens)	Richness (number of species)	Shannon diversity index
Young site	135±18 a	20±1.5 a	1.06±0.06 a
Middle-aged site	163±27 a	15±1.7 a	0.71±0.08 b
Old site	145±27 a	17±3.3 a	0.91±0.09 ab

Different letters in columns indicate significant differences (Mann–Whitney *U* Test, $p<0.05$)

29.1% of species variability, respectively. Soil P was the constraining variable with the highest score for the X axis (−0.84), with taxa to the right negatively correlated with the available P content of the soil organic horizon and consequently more abundant at the oldest site. The highest biplot score was obtained by soil C content for the second axis (0.69), with taxa to the top positively correlated with C content in the soil organic horizon and therefore associated to older sites. The diagram suggests that genera as *Hygrocybe*, *Gymnopus* or *Lepiota* are more dependent upon soil C and N contents and are more abundant when concentrations of these elements are smaller. In contrast, *Mycena* would be more dependent upon available P content, since its vector is almost parallel to the "P" axis. The equilibrium circle showed that the genera *Clitocybe, Cyathus, Galerina, Gymnopus, Hygrocybe, Hygrophoropsis, Hypholoma, Lepiota* and *Mycena* contributed significantly the the ordination biplot.

Spearman correlations showed no significant relationship between total abundance or richness and any of the measured soil variables. However, Shannon diversity index correlated significantly ($p=0.016$) with soil P content, as shown in Fig. 4. More precise correlations at the genus and species levels showed that saprophytic fungi respond differently to soil factors (Table 4). *Lepiota* sp. was the only species to be negatively correlated with C, N and P contents of the soil organic horizon, as it was suggested by the CCA biplot. *Hygrophoropsis aurantiaca* correlated significantly with soil available P. The genus *Hypholoma* as a whole was significantly and negatively correlated with the soil C:N ratio whereas *Hypholoma fasciculare* was not. On the other hand, *Clitocybe gibba* (Pers.) P. Kumm. correlated with the C:N ratio whereas the genus *Clitocybe* did not. Saprophytic fungal species distribution is influenced by soil factors, and specific responses exist to the different edaphic variables under study.

Discussion

Saprophytic communities at the three sites were mainly composed of rare taxa, with a small number of frequent species, which is in agreement with the findings of previous studies (Rubino and McCarthy 2003; Richard et al. 2004). These rare species are particularly relevant for decomposition processes and ecosystem functioning (Deacon et al. 2006). Most of the sampled species were basidiomycetes (96%). This proportion reflects the abundance of basidiomycetes in coniferous forests, where the accumulation of favorable substrates is likely to enhance the diversity of decomposer species (Ohlson et al. 1997). The conspicuous sporocarps of basidiomycete fungi may have biased the

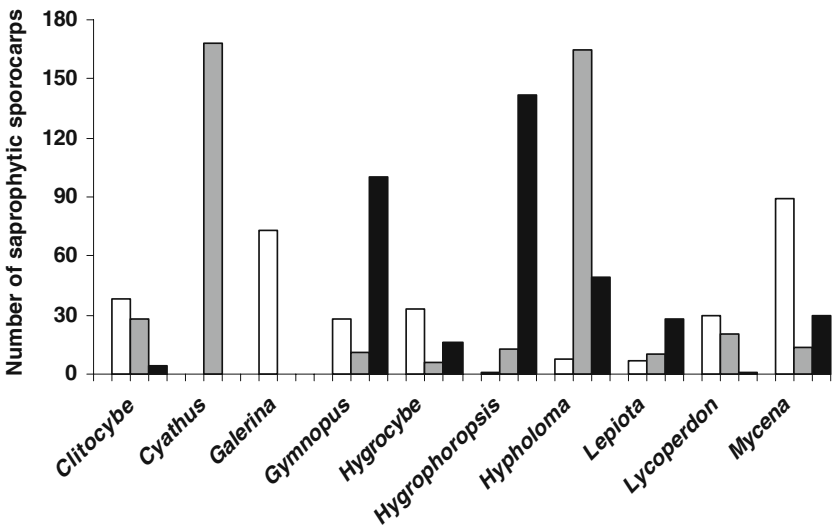

Fig. 1 Saprophytic macrofungi community composition by genus at the three study sites during three consecutive years. *White bars* represent the young site, *gray bars* the middle-aged site, *black bars* the old site

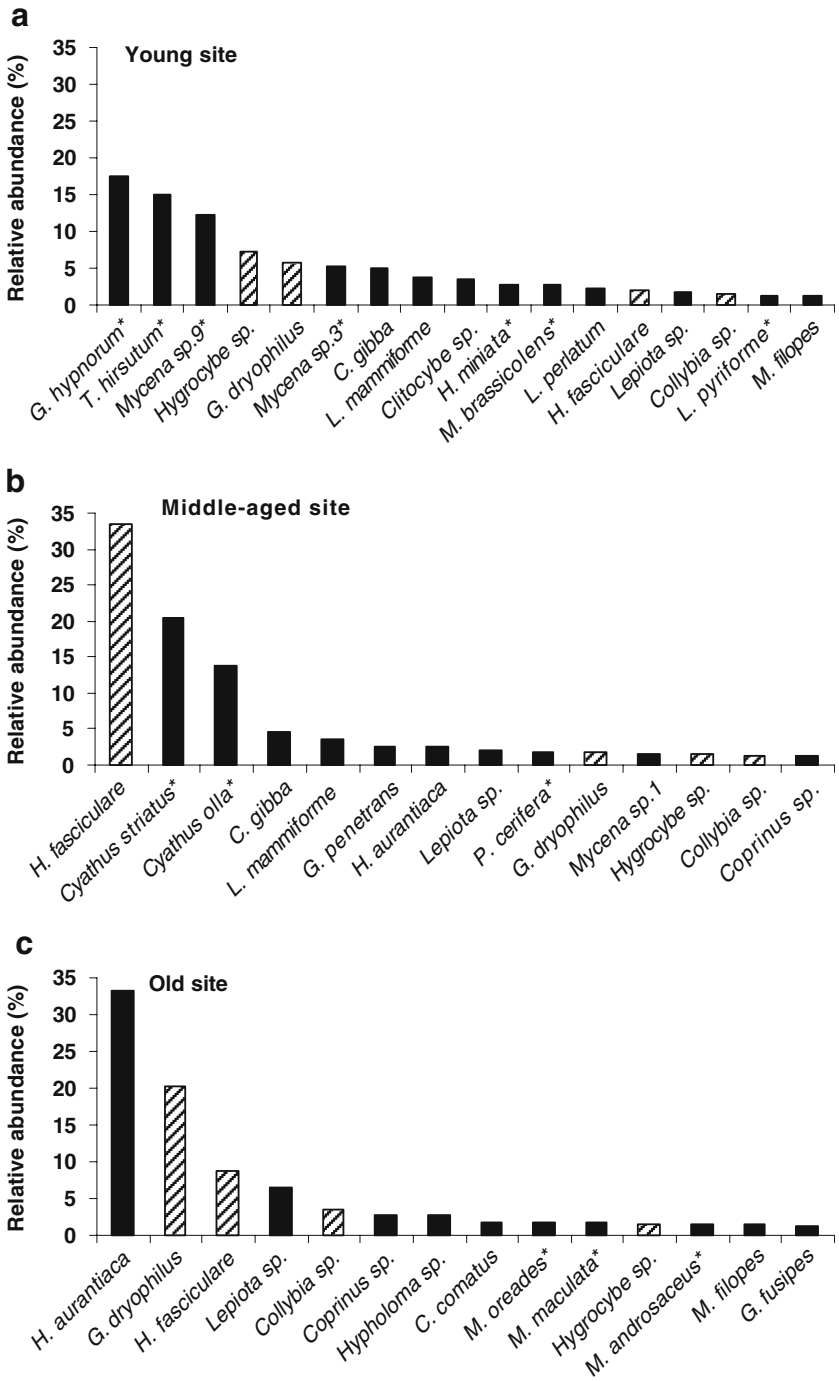

Fig. 2 Species relative abundance of saprophyte sporocarps at the three study sites. *Dashed bars* represent species common to the three sites. *C. gibba: Clitocybe gibba; C. comatus: Coprinus comatus; C. olla: Cyathus olla; C. striatus: Cyathus striatus; G. hypnorum: Galerina hypnorum; G. penetrans: Gymnopilus penetrans; G. spadiceus: Gymnopilus spadiceus; G. dryophilus: Gymnopus dryophilus; G. fusipes: Gymnopus fusipes; H. miniata: Hygrocybe miniata; H. aurantiaca: Hygrophoropsis aurantiaca; H. fasciculare: Hypholoma fasciculare; L. mammiforme: Lycoperdon mammiforme; L. perlatum: Lycoperdon perlatum; L. pyriforme: Lycoperdon pyriforme; M. androsaceus: Marasmius androsaceus; M. oreades: Marasmius oreades; M. brassicolens: Micromphale brassicolens; M. filopes: Mycena filopes; M. maculata: Mycena maculata; Myc. sp. 1*: *Mycena* sp. 1; *Myc. sp. 3*: *Mycena* sp. 3; *Myc. sp.4*: *Mycena* sp. 4; *Myc. sp. 9*: *Mycena* sp. 9; *P. cerifera: Pholiota cerifera; T. hirsutum: Trichoglossum hirsutum*

sampling towards this particular fungal class, although basidiomycete mycelia is reported to be ubiquitous in forest soils (Cairney 2005) and is therefore likely to play an important role in nutrient and carbon cycling processes (Dighton 2003).

The lack of significant differences in fungal abundance and richness between sites may be explained by the fact that saprophytic species are dependent on the type of litter covering the forest soil, and thus on the dominant species of the tree community (Senn-Irlet and Bieri 1999). In this study, we selected study sites dominated by *P. montezumae* in order to examine the changes in saprophytic communities due to soil factors only, and this may have led to this relative structure similarity. Precipitation and microclimate conditions were relatively constant across the three sites (Peña-Ramírez, unpublished data) and any change in sporocarp production is likely to be attributed to soil parameters. Diversity patterns and species composition

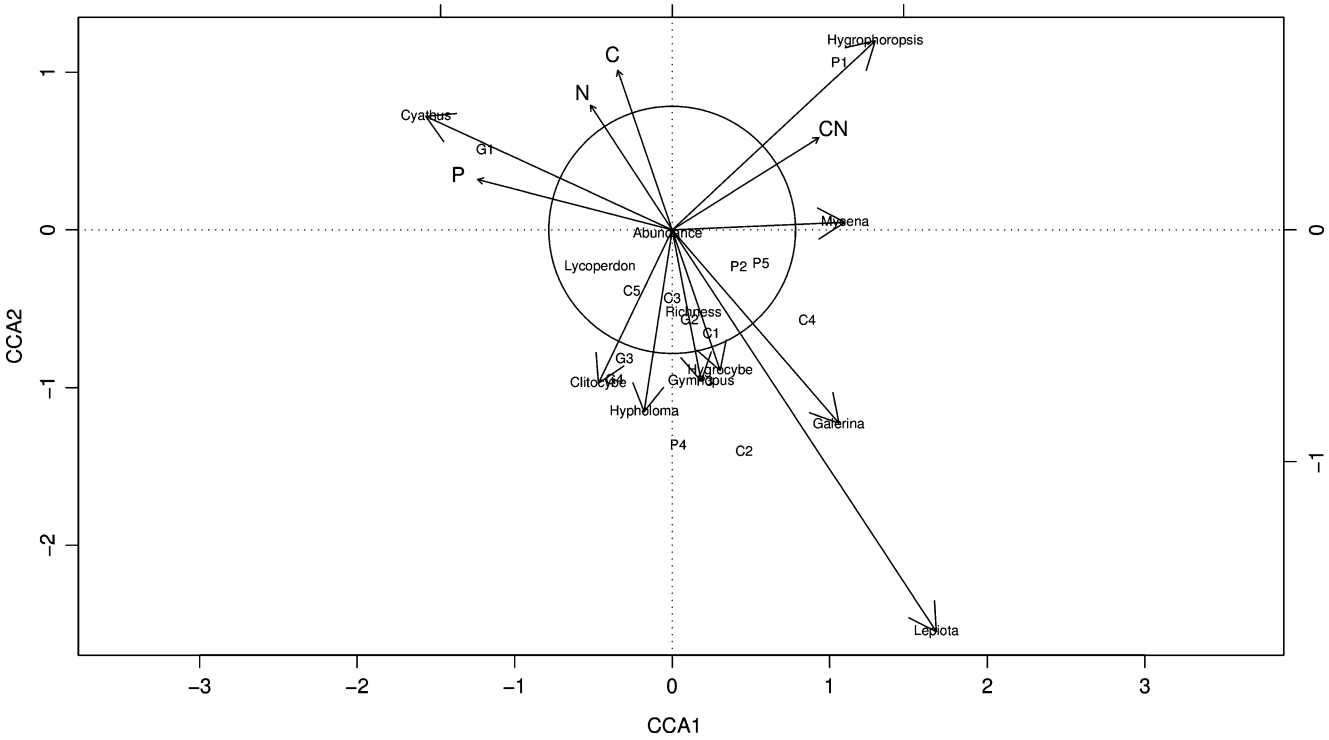

Fig. 3 CCA ordination biplot of saprophytic fungal genera based on their abundance at the three study sites, constrained by soil factors. Genera outside the equilibrium circle contribute significantly to the diagram. *Letters* represent the study sites (*C* Chichinautzin, *G* Guespalapa, *P* Pelado) and *numbers* represent the sampling plots (five plots per site)

varied across the soil chronosequence: the young site was dominated by species belonging to the genera *Galerina* and *Mycena*, whereas *Cyathus* spp. and *Hypholoma* spp. dominated at the middle-aged site and *Hygrophoropsis aurantiaca* was the most abundant species at the old site. These differences in species composition emphasize the importance of soil factors on fungal community composition. Soil humification processes and thickness of the litter layer are particularly relevant for terrestrial saprophytic fungi (Mihál and Bučinová 2005). Soil nutrient status has been shown to affect mycelial development and hence sporocarp occurrence (Donnelly and Boddy 1998; Zakaria and Boddy 2002; Harold et al. 2005). The soil organic horizon may be especially relevant since saprophytic fungi are reported to typically extend their mycelia at the soil–litter interface (Boddy et al. 2009). The nutrient status of soil environment through which decomposer fungi grow may determine their diversity as it influences mycelial outgrowth and network formation (Donnelly and Boddy 1998; Zakaria and Boddy 2002). In this study, only soil P content was found to correlate significantly with the Shannon diversity index, which corroborates the potential importance of saprophytic hyphae for P mobilization and phosphate hydrolysis. Nevertheless, fungal diversity increased when available P contents were lower, suggesting that more decomposer species are required when P is scarce in order to solubilize it, as saprophytic fungi tend to incorporate hydrolyzed phosphate into their biomass (Dighton 1983).

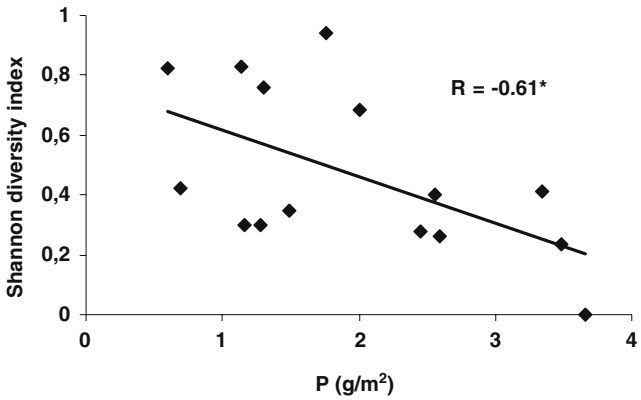

Fig. 4 Shannon diversity index by sampling plot in correlation with soil P (g/m^2). *R* Spearman correlation coefficient, *significant

Whether saprophytic species diversity reflects functional diversity is still unknown, although it is widely believed that many decomposer species are functionally redundant (Andrén et al. 1995; Deacon et al. 2006). An increased number of species may lead to an increased number of ecological functions and thus a more efficient degradation of recalcitrant substrates (Setälä and McLean 2004). However, a single species may play diverse roles and hence there may be no relationship between species diversity and functional diversity for fungal species (van

Table 4 Spearman correlation R values as traducing the relationship between saprophytic sporocarp genera and species with soil variables

	Soil C content (kg/m^2)	Soil N content (kg/m^2)	Soil P content (g/m^2)	Soil C:N ratio
Total abundance	−0.179	−0.172	−0.293	−0.236
Total richness	−0.313	−0.262	−0.459	−0.287
Shannon diversity	−0.332	−0.282	−0.611*	−0.418
Clitocybe spp.	−0.145	−0.095	−0.109	−0.492
Clitocybe gibba	0.023	0.067	−0.204	−0.577*
Cyathus spp.	0.124	0.186	0.186	−0.186
Cyathus striatus	0.124	0.186	0.186	−0.186
Galerina hypnorum	−0.247	−0.186	0.000	0.371
Gymnopus spp.	0.044	0.083	−0.353	−0.254
Gymnopus dryophilus	0.115	0.148	−0.217	−0.062
Hygrocybe spp.	−0.309	−0.274	−0.451	−0.097
Hygrophoropsis aurantiaca	0.087	0.053	−0.591*	−0.101
Hypholoma spp.	0.115	0.147	−0.344	−0.655*
Hypholoma fasciculare	0.232	0.271	−0.138	−0.454
Lepiota sp.	−0.600*	−0.595*	−0.541*	−0.079
Lycoperdon spp.	−0.131	−0.113	0.171	−0.171
Lycoperdon mammiforme	−0.045	−0.016	0.166	−0.166
Mycena spp.	−0.125	−0.161	−0.226	0.351
Mycena sp.6	0.045	0.091	0.045	−0.318

*Significant correlation at $p<0.05$

der Heijden et al. 1998). Deacon et al. (2006) emphasized the importance of species composition of the community rather than its richness or diversity, as this study suggests, since species interactions may enhance the decomposition of organic matter.

All the significant correlations between species abundance and soil variables were negative, which is consistent with the largest diversity values found at the youngest, less fertile site. The CCA biplot showed that most fungal taxa were distributed where soil C and N contents were lower, which is consistent with previous works reporting that a higher fungal diversity may lead to increased decomposition rates, and thus to lower organic matter contents (Deacon 1985; Robinson et al. 1993; Setälä and McLean 2004). However, different fungal species have divergent responses to soil factors, as also shown by the CCA diagram and by correlation analysis.

The highest species diversity of the decomposer community at the young site may have been enhanced by its greater spatial heterogeneity. A heterogeneous soil environment, typically found in young volcanic soils (Aplet et al. 1997) and generated by the large amount of volcanic rocks, creates an important number of microniches where more species should be able to find resources and suitable abiotic conditions (Sulkava and Huhta 1998). It may also have led to the important number of site-exclusive species at the young site. Similar patterns were observed in ectomycorrhizal (ECM) fungal communities (Reverchon et al., in preparation), since ECM species richness and number of site-exclusive species were higher at Chichinautzin. Increased species number in diverse communities may act as "insurance" against harsh environmental conditions (Naeem, 1998) as those present at the young, heterogeneous, and less fertile site.

Conclusion

Saprophytic fungal communities vary according to soil factors across the volcanic soil chronosequence. They were found to be more diverse at the youngest site, where spatial heterogeneity was larger and soil nutrient status lower than at the older sites. However, fungal responses to soil factors differed according to the species considered, which generated changes in community composition at the three sites. The high percentage of site-exclusive species showed that species composition was strongly dependent upon the site and thus upon soil parameters. The highest diversity found at the young, less fertile site may represent an "insurance" mechanism against harsh conditions, since different species are likely to play various ecological functions which may lead to a more efficient degradation of recalcitrant substrates. Understanding the factors involved in the distribution and diversity of decomposer fungi results will be useful for conservation

and inventory purposes, and this is especially relevant for young volcanic soils, where published information on how fungal communities are organized is scarce.

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References

Andrén O, Clarholm M, Bengtsson J (1995) Biodiversity and species redundancy among litter decomposers. In: Collins HP, Robertson GP, Klug MJ (eds) The Significance and Regulation of Soil Biodiversity. Kluwer, Dordrecht, pp 141–151

Aplet GH, Hughes RF, Vitousek PM (1997) Ecosystem development on Hawaiian lava flows: biomass and species composition. J Veg Sci 9:17–26

Boddy L, Hynes J, Bebber DP, Fricker MD (2009) Saprotrophic cord systems: dispersal mechanisms in space and time. Mycoscience 50:9–19

Bon M (2004) Champignons de France et d´Europe occidentale. Flammarion, France

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

Cairney JWG (2005) Basidiomycete mycelia in forest soils: dimensions, dynamics and roles in nutrient distribution. Mycol Res 109:7–20

Deacon JW (1985) Decomposition of filter paper cellulose by thermophilic fungi acting singly, in combination, and in sequence. Trans Br Mycol Soc 85:663–669

Deacon LJ, Pryce-Miller EJ, Frankland JC, Bainbridge BW, Moore PD, Robinson CH (2006) Diversity and function of decomposer fungi from a grassland soil. Soil Biol Bioch 38:7–20

Dighton J (1983) Phosphatase production by mycorrhizal fungi. Plant Soil 71:455–462

Dighton J (2003) Fungi in Ecosystem Processes. Marcel Dekker, New York

Dix NJ, Webster J (1995) Fungal ecology. Chapman & Hall, London

Donnelly DP, Boddy L (1998) Developmental and morphological responses of mycelial systems of *Stropharia caerulea* and *Phanerochaete velutina* to soil nutrient enrichment. New Phytol 138:519–531

Gebauer G, Taylor AFS (1999) ^{15}N natural abundance in fruit bodies of different functional groups of fungi in relation to substrate utilization. New Phytol 142:93–101

Harold S, Tordoff GM, Jones TH, Boddy L (2005) Mycelial responses of *Hypholoma fasciculare* to collembola grazing: effect of inoculum age, nutrient status and resource quality. Mycol Res 109(8):927–935

Hedger J (1985) Tropical agarics, resource relations and fruiting periodicity. In: Moore D, Casselton LA, Wood DA, Frankland JC (eds) Developmental Biology of Higher Plants. Cambridge University Press, Cambridge, pp 41–86

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

Kuyper TW, Verschoor BC (1995) Enhancement of nitrification rates in vitro by interacting species of saprotrophic fungi. Mycol Res 99:1128–1130

Laessøe T, Ryvarden L, Watling R, Whalley AJS (1996) Saprotrophic fungi of the Guinea - Congo Region. Proc R Soc Edinburgh 104B:335–347

Lodge DJ (1997) Factors related to diversity of decomposer fungi in tropical forests. Biodivers Conserv 6:681–688

Lodge DJ, Cantrell S (1995) Fungal communities in wet tropical forests: variation in time and space. Can J Bot 73:S1391–S1398

Márquez A, Verma SP, Anguita F, Oyarzun R, Brandle JL (1999) Tectonics and volcanism of Sierra Chichinautzin: extension at the front of the Central Trans—Mexican Volcanic belt. J Volcanol Geotherm Res 93:125–150

Mihál I, Bučinová K (2005) Species diversity, abundance and dominance of macromycetes in beech forest stands. J For Sc 51(5):187–194

Naeem S (1998) Species redundancy and ecosystem reliability. Conserv Biol 12:39–45

Ohlson M, Söderström L, Hörnberg G, Zackrisson O, Hermansson J (1997) Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. Biol Conserv 81:221–231

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

Petersen RH, Cifuentes J (1994) Notes on mating systems of *Auriscalpium vulgare* and *A. villipes*. Mycol Res 98:1427–1430

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

Robinson CH, Dighton J, Frankland JC, Coward PA (1993) Nutrient and carbon dioxide release by interacting species of straw-decomposing fungi. Plant Soil 151:139–142

Rubino DL, McCarthy BC (2003) Composition and ecology of macrofungal and myxomycete communities on oak woody debris in a mixed-oak forest of Ohio. Can J For Res 33:2151–2163

Schimel JP, Gulledge JM, Clein-Curley JS, Lindstrom JE, Braddock JF (1999) Moisture effects on microbial activity and community structure in decomposing birch litter in the Alaskan taiga. Soil Biol Biochem 31:831–838

Senn-Irlet B, Bieri G (1999) Sporocarp succession of soil-inhabiting macrofungi in an autochtonous subalpine Norway spruce forest of Switzerland. For Ecol Manag 124:169–175

Setälä H, McLean MA (2004) Decomposition rate of organic substrates in relation to the species diversity of soil saprophytic fungi. Oecologia 139:98–107

Siebe C, Rodríguez-Lara V, Schaaf P, Abrams M (2004) Radiocarbon ages of Holocene Pelado, Guespalapa, and Chichinautzin scoria cones, south of Mexico City: Implications for archaeology and future hazards. Bull Volcanol 66:203–225

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

Steffen KT, Hofrichter M, Hatakka A (2000) Mineralisation of ^{14}C-labelled synthetic lignin and ligninolytic enzyme activities of litter-decomposing basidiomycetous fungi. Appl Microbiol Biotechnol 54:819–825

Sulkava P, Huhta V (1998) Habitat patchiness affects decomposition and faunal diversity: a microcosm experiment on forest floor. Oecologia 116:390–396

van der Heijden MGA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396:69–72

Velázquez A (1994) Multivariate analysis of the vegetation of the volcanoes Tláloc and Pelado, Mexico. J Veg Sci 5:263–270

World Reference Base (WRB) 2006 World Reference Base for Soil Resources, second edn. World Soil Resources Reports No. 103. FAO, Rome

Zakaria AJ, Boddy L (2002) Mycelial foraging by *Resinicium bicolor*: interactive effects of resource quantity, quality and soil composition. FEMS Microbiol Ecol 40:135–142