ORIGINAL ARTICLE

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

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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 1835 years B.P. to 10000 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.

Key words: saprophytic fungi, volcanic soil chronosequence, fungal diversity, community structure.

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 (1835 years B.P.), the middle-aged Guespalapa volcano (4200 years B.P.) and the oldest Pelado volcano (10000 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 3100 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.

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 did influence significantly 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 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 1331 specimens were collected during the three 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*.

Table 2

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 the 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, 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 neither abundance nor 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 resulted to be 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.

Table 3

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 of saprophytic species were only found at the youngest site. Those belonged to the fungal genera *Galerina*, *Hygrocybe* and *Mycena*, whereas species as *Cyathus olla* (Batsch) Pers. and *Cyathus striatus* (Huds.) Willd. were exclusive of the middle-

aged site and *Marasmius 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 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.

Fig. 1

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 (Figs. 2b and 2c). 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. On the contrary, 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 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. On the contrary, *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 to the ordination biplot. Fig 3

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 *Hypholomola 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. Fig. 4 Table 4

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 MacCarthy, 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 favourable substrates is likely to enhance the diversity of decomposer species (Ohlson *et al*., 1997). The conspicuous sporocarps of basidiomycete fungi may have biased the 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 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 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 hydrolysed phosphate into their biomass (Dighton, 1983).

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

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FIGURE CAPTIONS.

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; 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.*

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).

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

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.*)	1835 ± 55					2835 ± 75 to 4690 ± 90					9620 ± 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	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	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	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	2.13 ± 0.37[ab]					2.39 ± 0.29[a]					1.38 ± 0.19[b]				

* 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).

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.*			1						
Agrocybe sp.*								1	
Clitocybe aff. costata Kühner & Romagn.*		1							
Clitocybe aff. dealbata (Sowerby) Gillet*				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*								1	
Coprinus comatus (O.F. Müll.) Pers.					3	1		8	
Coprinus aff. cortinatus J.E. Lange*							4		
Coprinus sp.				4	2			12	
Cyathus olla (Batsch) Pers.*				10	58				
Cyathus striatus (Huds.) Willd.*				100					
Galerina aff. hypnorum (Schrank) Kühner*	5	38	30						
Geoglossum cookeanum Nannf.*	2								
Gymnopilus penetrans (Fr.) Murrill					13			2	
Gymnopilus aff. spadiceus Romagn.*	4								
Gymnopilus sp.			1						2
Gymnopus acervatus (Fr.) Murrill*		3							
Gymnopus aff. confluens (Pers.) Antonín, Halling & Noordel.*								2	
Gymnopus dryophilus (Bull.) Murrill	5	5	14	5	3	1	16	43	28
Gymnopus erythropus (Pers.) Antonín, Halling & Noordel.*		1							
Gymnopus aff. fusipes (Bull.) Gray						2		5	
Gymnopus aff. peronatus (Bolton) Antonín, Halling & Noordel.*							2		
Gymnopus aff. perforans (Hoffm.) Antonín & Noordel*									4
Hygrocybe miniata (Fr.) P. Kumm.*		1	10						
Hygrocybe persistens var. konradii (R. Haller Aar.) Boertm.*	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.*					3				
Lycoperdon mammiforme Pers.	5	5	6	7	4	6			
Lycoperdon perlatum Pers.	3	4	2			3			
Lycoperdon pyriforme Schaeff.*	5								
Lycoperdon umbrinum Pers.*							1		

Marasmius aff. alliaceus (Jacq.) Fr.*					1	1			
Marasmius aff. androsaceus (L.) Fr.*								6	
Marasmius oreades (Bolton) Fr.*							2	6	
Marasmius sp.		2			2	1		1	
Micromphale aff. brassicolens var. brassicolens (Romagn.) P.D. Orton*	11								
Mycena aff. epipterygia (Scop.) Gray*								3	1
Mycena aff. filopes (Bull.) P. Kumm.		3	2					1	5
Mycena aff. galericulata (Scop.) Gray*								2	
Mycena aff. maculata P. Karst.*								7	
Mycena aff. metata (Secr. ex Fr.) P. Kumm.*	2								
Mycena aff. pura (Pers.) P. Kumm.		1	1				4		
Mycena sp.1					5	2	2		
Mycena sp.2		1					3		
Mycena sp.3*	12	10							
Mycena sp.4*	4								
Mycena sp.5*							1		
Mycena sp.6				1			1		
Mycena sp.7*				2					
Mycena sp.8*		2							
Mycena sp.9*		49	2						
Mycena sp.10*					4				
Panaeolus sp.*		1							
Peziza sp.*		1							
Pholiota cerifera P. Karst.*				9					
Pholiota sp.*							3		
Pluteus cervinus P. Kumm.*								1	
Pluteus sp.*									1
Psathyrella sp.*				3					
Ramaria stricta (Pers.) Quél.*							2		
Rhodocollybia aff. butyracea (Bull.) Lennox			3			3			
Stropharia sp.*			3						
Trichoglossum hirsutum var. hirsutum (Pers.) Boud.*	17	30	15						
Tricholomopsis rutilans (Schaeff.) Singer*		2							
Tricholomopsis sp.*				1					

* Site-exclusive species.

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

TABLE 3 - Annual abundance, richness and diversity of the community of saprophyte sporocarps at the three sites.

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

Note: Different letters mean significant differences (Mann-Whitney U Test, $p < 0.05$).

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 $p < 0.05$.

FIG. 1

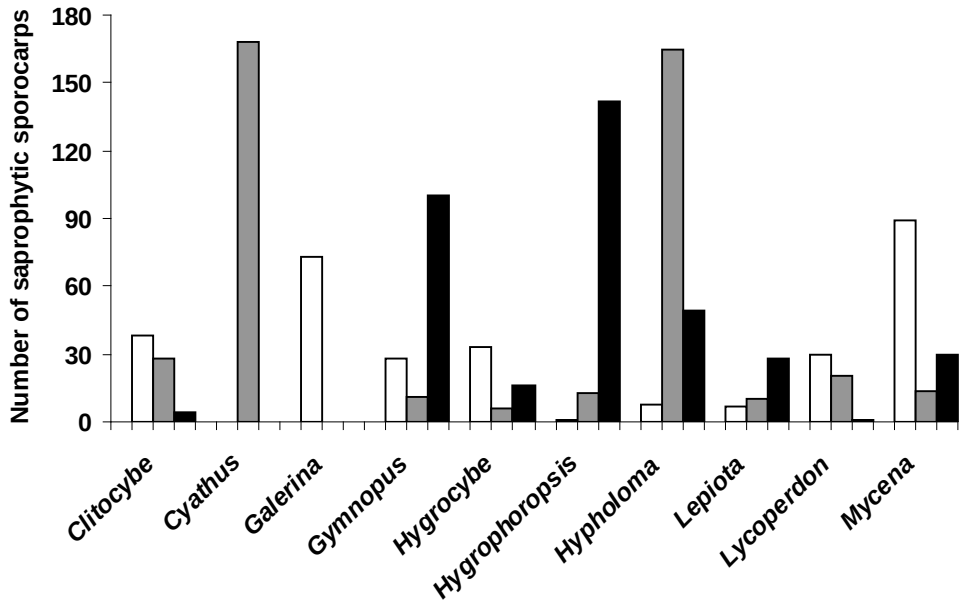
Number of saprophytic sporocarps
180
150
120
90
60
30
0
Clitocybe
Cyathus
Galerina
Gymnopus
Hygrocybe
Hygrophoropsis
Hypholoma
Lepiota
Lycoperdon
Mycena

FIG. 2

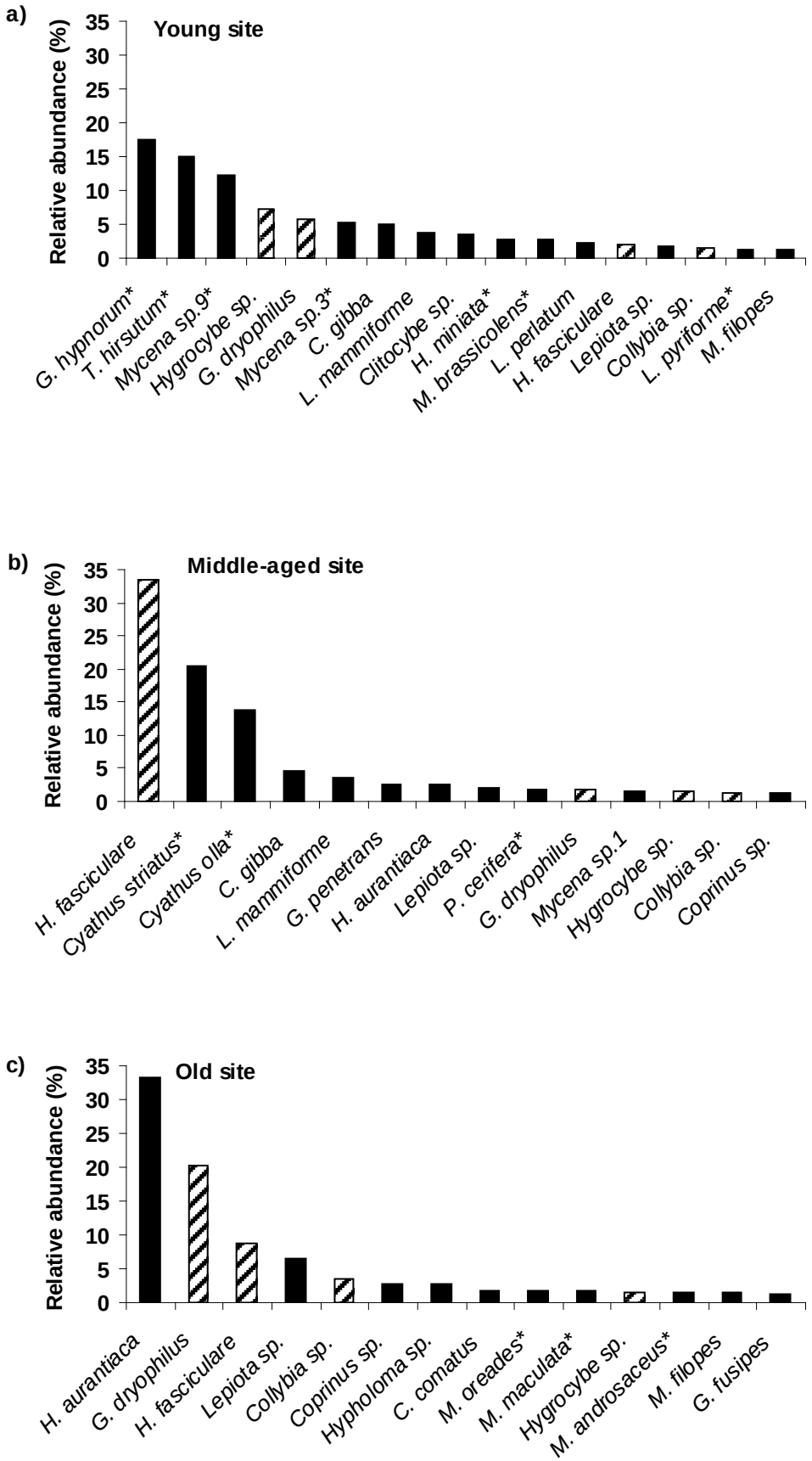
a)
Young site
Relative abundance (%)
35
30
25
20
15
10
5
0
G. hypnorum*
T. hirsutum*
Mycena sp.9*
Hygrocybe sp.
G. dryophilus
Mycena sp.3*
C. gibba
L. mammiforme
Clitocybe sp.
H. miniata*
M. brassicolens*
L. perlatum
H. fasciculare
Lepiota sp.
Collybia sp.
L. pyriforme*
M. filopes
b)
Middle-aged site
Relative abundance (%)
35
30
25
20
15
10
5
0
H. fasciculare
Cyathus striatus*
Cyathus olla*
C. gibba
L. mammiforme
G. penetrans
H. aurantiaca
Lepiota sp.
P. cerifera*
G. dryophilus
Mycena sp.1
Hygrocybe sp.
Collybia sp.
Coprinus sp.
c)
Old site
Relative abundance (%)
35
30
25
20
15
10
5
0
H. aurantiaca
G. dryophilus
H. fasciculare
Lepiota sp.
Collybia sp.
Coprinus sp.
Hypholoma sp.
C. comatus
M. oreades*
M. maculata*
Hygrocybe sp.
M. androsaceus*
M. filopes
G. fusipes

FIG. 3

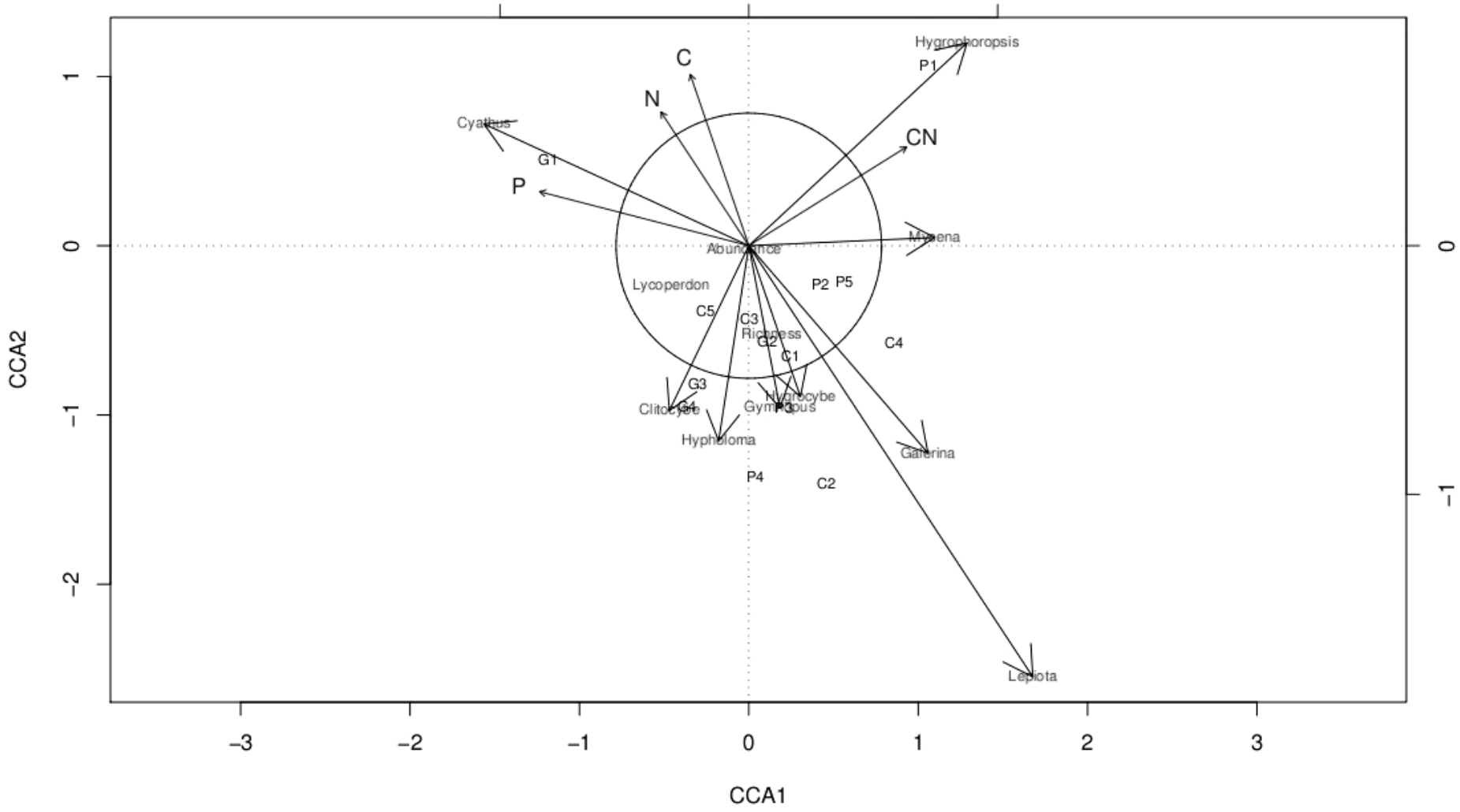
Hygrophoropsis
P1
C
N
CN
Cyathus
G1
P
Mycena
Abundance
Lycoperdon
P2
P5
C5
C3
Richness
G2
C1
C4
G3
Hygrocybe
Clitocybe
G4
Gymnopus
Hypholoma
Galerina
P4
C2
Lepiota
CCA1
CCA2
−3
−2
−1
0
1
2
3
1
0
−1
−2

FIG. 4