1 **ORIGINAL ARTICLE**

2
3 **Saprophytic fungal communities change in diversity and species**
4 **composition across a volcanic soil chronosequence at Sierra del**
5 **Chichinautzin, Mexico**

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22 **Abstract** - Saprophytic fungi are one of the most active decomposers of forest
23 litter, and their diversity may be influenced by the spatial heterogeneity of
24 substrates. We examined the changes in saprophytic community structure and
25 composition across a volcanic soil chronosequence, at Sierra del Chichinautzin,
26 Mexico. Saprophytic fungi were collected for three consecutive years at three
27 sampling sites with contrasting soil properties in a volcanic soil chronosequence
28 ranging from 1835 years B.P. to 10000 years B.P. Although no significant
29 differences were found in terms of abundance and richness between the three
30 sites, Shannon diversity was higher at the youngest, less-fertile site. The high
31 percentage of site-exclusive species showed that species composition was
32 strongly dependent on the site and therefore on soil parameters. Different
33 saprophytic species had divergent responses to soil variables, but most fungal
34 taxa correlated negatively with the edaphic factors we measured. The highest

1 diversity found at the young, less fertile site may represent an “insurance”
2 mechanism against harsh conditions, since different species are likely to play
3 various ecological functions which may lead to a more efficient degradation of
4 recalcitrant substrates.

5
6 **Key words:** saprophytic fungi, volcanic soil chronosequence, fungal diversity,
7 community structure.

1 INTRODUCTION

2
3 Saprophytic fungi are one of the most active decomposers of forest litter and
4 therefore play an important role in the cycling of carbon, nitrogen, and other soil
5 nutrients (Smith and Read, 2008). Basidiomycetes are reported to be especially
6 important for organic matter decomposition as they produce a wide range of
7 ligninocellulolytic enzymes (Dix and Webster, 1995). Although most substrates
8 can be decomposed by many fungal species, the decomposition ability of each
9 species varies depending on environmental conditions (Deacon, 1985; Schimel *et al.*,
10 1999) and on interactions with other fungi (Robinson *et al.*, 1993; Kuyper
11 and Verschoor, 1995). It is acknowledged that the presence of specific taxa
12 depends on the type and quality of litter available (Steffen *et al.*, 2000),
13 although scarce information has been provided about the association of particular
14 saprophytic species with particular types of soil.

15 Species composition of saprophytic fungal communities could determine the
16 extent of organic matter decomposition, since different fungal species perform
17 different ecological functions (Setälä and McLean, 2004; Deacon *et al.*, 2006)
18 and occupy complementary niches (Hedger, 1985). Different microhabitats or
19 substrates could influence, in turn, the diversity of decomposer fungi (Lodge and
20 Cantrell, 1995; Laessøe *et al.*, 1996), especially since soil nutrients are often
21 patchily distributed (Boddy *et al.*, 2009). This patchy distribution is particularly
22 critical in volcanic soils presenting a high spatial heterogeneity (Aplet *et al.*,
23 1997). The discontinuous cover of young volcanic soils by lava flows creates a
24 large amount of microniches, which in turn could enhance fungal diversity
25 (Lodge, 1997; Sulkava and Huhta, 1998).

26 Owing to the lack of mutualistic interaction with higher plants, saprophytes
27 are expected to be more dependent upon their respective substrates than are
28 mycorrhizal fungi (Gebauer and Taylor, 1999) and could therefore be influenced
29 by abiotic factors such as soil nutrients or soil moisture (Zakaria and Boddy,
30 2002; Richard *et al.*, 2004). In order to examine the effect of soil factors on
31 saprophyte fungal communities, we assessed the abundance, richness and
32 diversity patterns of those communities across a volcanic soil chronosequence,
33 where the different stages of pedogenesis generated contrasting soil properties.
34 As soil develops, its nutrient status changes and soil quality as a whole improves
35 (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.

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*.

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.

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-

Fig. 1

Fig. 2

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.

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* (Schränk) 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*.

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.

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.

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

1 type of litter covering the forest soil, and thus on the dominant species of the
2 tree community (Senn-Irlet and Bieri, 1999). In this study, we selected study
3 sites dominated by *P. montezumae* in order to examine the changes in
4 saprophytic communities due to soil factors only, and this may have led to this
5 relative structure similarity. Precipitation and microclimate conditions were
6 relatively constant across the three sites (Peña-Ramírez, unpublished data) and
7 any change in sporocarp production is likely to be attributed to soil parameters.
8 Diversity patterns and species composition varied across the soil
9 chronosequence: the young site was dominated by species belonging to the
10 genera *Galerina* and *Mycena*, whereas *Cyathus* spp. and *Hypholoma* spp.
11 dominated at the middle-aged site and *Hygrophoropsis aurantiaca* was the most
12 abundant species at the old site. These differences in species composition
13 emphasize the importance of soil factors on fungal community composition. Soil
14 humification processes and thickness of the litter layer are particularly relevant
15 for terrestrial saprophytic fungi (Mihál and Bučinová, 2005). Soil nutrient status
16 has been shown to affect mycelial development and hence sporocarp occurrence
17 (Donnelly and Boddy, 1998; Zakaria and Boddy, 2002; Harold *et al.*, 2005). The
18 soil organic horizon may be especially relevant since saprophytic fungi are
19 reported to typically extend their mycelia at the soil-litter interface (Boddy *et al.*,
20 2009). The nutrient status of soil environment through which decomposer fungi
21 grow may determine their diversity as it influences mycelial outgrowth and
22 network formation (Donnelly and Boddy, 1998; Zakaria and Boddy, 2002). In
23 this study, only soil P content was found to correlate significantly with Shannon
24 diversity index, which corroborates the potential importance of saprophytic
25 hyphae for P mobilization and phosphate hydrolysis. Nevertheless, fungal
26 diversity increased when available P contents were lower, suggesting that more
27 decomposer species are required when P is scarce in order to solubilize it, as
28 saprophytic fungi tend to incorporate hydrolysed phosphate into their biomass
29 (Dighton, 1983).

30 Whether saprophytic species diversity reflects functional diversity is still
31 unknown, although it is widely believed that many decomposer species are
32 functionally redundant (Andrén *et al.*, 1995; Deacon *et al.*, 2006). An increased
33 number of species may lead to an increased number of ecological functions and
34 thus a more efficient degradation of recalcitrant substrates (Setälä and McLean,
35 2004). However, a single species may play diverse roles and hence there may be

1 no relationship between species diversity and functional diversity for fungal
2 species (van der Heijden *et al.*, 1998). Deacon *et al.* (2006) emphasized the
3 importance of species composition of the community rather than its richness or
4 diversity, as this study suggests, since species interactions may enhance the
5 decomposition of organic matter.

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

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

29 **CONCLUSION**

31 Saprophytic fungal communities vary according to soil factors across the volcanic
32 soil chronosequence. They were found to be more diverse at the youngest site,
33 where spatial heterogeneity was larger and soil nutrient status lower than at the
34 older sites. However, fungal responses to soil factors differed according to the
35 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*: *Gymnopilus 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/m²). 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 ¹⁴C 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
<i>Agaricus</i> sp. *			1						
<i>Agrocybe</i> sp. *								1	
<i>Clitocybe</i> aff. <i>costata</i> Kühner & Romagn.*		1							
<i>Clitocybe</i> aff. <i>dealbata</i> (Sowerby) Gillet*				4					
<i>Clitocybe gibba</i> (Pers.) P. Kumm.	2	3	16	14	4	5	2	1	
<i>Clitocybe</i> aff. <i>squamulosa</i> (Pers.) Fr.	1								1
<i>Clitocybe</i> sp.	2		13		1				
<i>Collybia</i> sp.	6			5	1		5	4	6
<i>Coprinopsis atramentaria</i> (Bull.) Readhead, Vilgalys & Moncalvo*								1	
<i>Coprinus comatus</i> (O.F. Müll.) Pers.					3	1		8	
<i>Coprinus</i> aff. <i>cortinatus</i> J.E. Lange*							4		
<i>Coprinus</i> sp.				4	2			12	
<i>Cyathus olla</i> (Batsch) Pers.*				10	58				
<i>Cyathus striatus</i> (Huds.) Willd.*				100					
<i>Galerina</i> aff. <i>hypnorum</i> (Schränk) Kühner*	5	38	30						
<i>Geoglossum cookeanum</i> Nannf. *	2								
<i>Gymnopilus penetrans</i> (Fr.) Murrill					13			2	
<i>Gymnopilus</i> aff. <i>spadiceus</i> Romagn.*	4								
<i>Gymnopilus</i> sp.			1						2
<i>Gymnopus acervatus</i> (Fr.) Murrill *		3							
<i>Gymnopus</i> aff. <i>confluens</i> (Pers.) Antonín, Halling & Noordel.*								2	
<i>Gymnopus dryophilus</i> (Bull.) Murrill	5	5	14	5	3	1	16	43	28
<i>Gymnopus erythropus</i> (Pers.) Antonín, Halling & Noordel.*		1							
<i>Gymnopus</i> aff. <i>fusipes</i> (Bull.) Gray						2		5	
<i>Gymnopus</i> aff. <i>peronatus</i> (Bolton) Antonín, Halling & Noordel.*							2		
<i>Gymnopus</i> aff. <i>perforans</i> (Hoffm.) Antonín & Noordel*									4
<i>Hygrocybe miniata</i> (Fr.) P. Kumm.*		1	10						
<i>Hygrocybe persistens</i> var. <i>konradii</i> (R. Haller Aar.) Boertm.*	1								
<i>Hygrocybe</i> sp.	12	3	6	6			12	4	
<i>Hygrophoropsis aurantiaca</i> (Wulfen) Maire	1			3	10		99	25	18
<i>Hypholoma fasciculare</i> var. <i>fasciculare</i> (Huds.) P. Kumm.		3	5	10	80	74	17	10	10
<i>Hypholoma</i> sp.				1			12		
<i>Lepiota</i> sp.	7				1	9	1	8	19
<i>Lepista flaccida</i> (Sowerby) Pat.*					3				
<i>Lycoperdon mammiforme</i> Pers.	5	5	6	7	4	6			
<i>Lycoperdon perlatum</i> Pers.	3	4	2			3			
<i>Lycoperdon pyriforme</i> Schaeff.*	5								
<i>Lycoperdon umbrinum</i> Pers.*							1		

<i>Marasmius aff. alliaceus</i> (Jacq.) Fr.*				1	1			
<i>Marasmius aff. androsaceus</i> (L.) Fr.*							6	
<i>Marasmius oreades</i> (Bolton) Fr.*						2	6	
<i>Marasmius</i> sp.	2			2	1		1	
<i>Micromphale aff. brassicolens</i> var. <i>brassicolens</i> (Romagn.) P.D. Orton*	11							
<i>Mycena aff. epipterygia</i> (Scop.) Gray*							3	1
<i>Mycena aff. filopes</i> (Bull.) P. Kumm.		3	2				1	5
<i>Mycena aff. galericulata</i> (Scop.) Gray*							2	
<i>Mycena aff. maculata</i> P. Karst.*							7	
<i>Mycena aff. metata</i> (Secr. ex Fr.) P. Kumm.*	2							
<i>Mycena aff. pura</i> (Pers.) P. Kumm.		1	1				4	
<i>Mycena</i> sp.1				5	2		2	
<i>Mycena</i> sp.2		1					3	
<i>Mycena</i> sp.3*	12	10						
<i>Mycena</i> sp.4*	4							
<i>Mycena</i> sp.5 *							1	
<i>Mycena</i> sp.6				1			1	
<i>Mycena</i> sp.7 *				2				
<i>Mycena</i> sp.8*		2						
<i>Mycena</i> sp.9 *		49	2					
<i>Mycena</i> sp.10 *					4			
<i>Panaeolus</i> sp.*		1						
<i>Peziza</i> sp.*		1						
<i>Pholiota cerifera</i> P. Karst.*				9				
<i>Pholiota</i> sp.*							3	
<i>Pluteus cervinus</i> P. Kumm.*								1
<i>Pluteus</i> sp.*								1
<i>Psathyrella</i> sp.*				3				
<i>Ramaria stricta</i> (Pers.) Quél.*							2	
<i>Rhodocollybia aff. butyracea</i> (Bull.) Lennox			3			3		
<i>Stropharia</i> sp.*			3					
<i>Trichoglossum hirsutum</i> var. <i>hirsutum</i> (Pers.) Boud.*	17	30	15					
<i>Tricholomopsis rutilans</i> (Schaeff.) Singer*		2						
<i>Tricholomopsis</i> 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 content (kg/m ²)	C Soil content (kg/m ²)	N Soil content (g/m ²)	P Soil ratio	C:N
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	
<i>Clitocybe</i> spp.	-0.145	-0.095	-0.109	-0.492	
<i>Clitocybe gibba</i>	0.023	0.067	-0.204	-0.577*	
<i>Cyathus</i> spp.	0.124	0.186	0.186	-0.186	
<i>Cyathus striatus</i>	0.124	0.186	0.186	-0.186	
<i>Galerina hypnorum</i>	-0.247	-0.186	0.000	0.371	
<i>Gymnopus</i> spp.	0.044	0.083	-0.353	-0.254	
<i>Gymnopus dryophilus</i>	0.115	0.148	-0.217	-0.062	
<i>Hygrocybe</i> spp.	-0.309	-0.274	-0.451	-0.097	
<i>Hygrophoropsis aurantiaca</i>	0.087	0.053	-0.591*	-0.101	
<i>Hypholoma</i> spp.	0.115	0.147	-0.344	-0.655*	
<i>Hypholoma fasciculare</i>	0.232	0.271	-0.138	-0.454	
<i>Lepiota</i> sp.	-0.600*	-0.595*	-0.541*	-0.079	
<i>Lycoperdon</i> spp.	-0.131	-0.113	0.171	-0.171	
<i>Lycoperdon mammiforme</i>	-0.045	-0.016	0.166	-0.166	
<i>Mycena</i> spp.	-0.125	-0.161	-0.226	0.351	
<i>Mycena</i> sp.6	0.045	0.091	0.045	-0 ; 318	

* Significant correlation at $p < 0.05$.

FIG. 1

FIG. 2

FIG. 3

FIG. 4