Diversity and fruiting patterns of ectomycorrhizal and saprobic fungi in an old-growth Mediterranean forest dominated by *Quercus ilex* L.

F. Richard, P.-A. Moreau, M.-A. Selosse, and M. Gardes

Abstract: We collected and mapped epigeous fruitbodies of both ectomycorrhizal (ECM) and saprobic fungi in an old-growth *Quercus ilex* L. Mediterranean forest within a permanent transect of 6400 m^2 over three consecutive fruiting seasons. Out of 5382 fruitbodies, a total of 234 species were found, including 166 and 68 ECM and saprobic taxa, respectively. Both communities were mainly composed of rare species. Two genera, *Russula* and *Cortinarius*, accounted for 34.4% of ECM fruitbodies and 50% of species diversity. The three most abundant ECM species were *Laccaria laccata* (Scop.: Fr.) Berk. & Broome, *Inocybe tigrina* R. Heim, and *Lactarius chrysorrheus* Fr. The fruiting ECM community encompassed a few Mediterranean species and numerous broad host range temperate species. We also analysed the fruiting patterns in relation to forest structure, host composition, and natural canopy gaps. The results showed (*i*) a significant correlation of species richness to tree density, (*ii*) a richness decrease as the number of vegetation layers increases, and (*iii*) a preferential fruiting of some species near *Q. ilex* or *Arbutus unedo* L. Another noteworthy feature was that richness and production were greatly enhanced in canopy gaps. Selective fruiting was also observed among species. These results highlight the importance of forest structure and large woody debris for fungal conservation.

Key words: ECM community, saprophytic fungi, holm oak, macromycete fruiting patterns, canopy gaps, fungal conservation.

Résumé : Nous avons récolté et cartographié les fructifications épigées de champignons ectomycorhiziens (ECM) et saprophytiques dans une vieille forêt méditerranéenne de *Quercus ilex* L. au sein d'un transect permanent de 6400 m^2, au cours de trois saisons consécutives de fructification. À partir de 5382 fructifications, nous avons reconnu 234 espèces incluant 166 espèces ectomycorhiziennes et 68 saprophytiques. Les deux communautés étaient principalement composées d'espèces rares. Les genres *Russula* and *Cortinarius* représentaient 34.4% des fructifications et 50% de la diversité ectomycorrhizienne. Les trois espèces ectomycorhiziennes les plus abondantes étaient *Laccaria laccata* (Scop.: Fr.) Berk. & Broome, *Inocybe tigrina* R. Heim et *Lactarius chrysorrheus* Fr. La communauté ectomycorhizienne était constituée de quelques espèces à affinités méditerranéennes et de nombreuses espèces tempérées à large spectre d'hôtes. Nous avons également examiné les relations entre les patrons de fructification et la structure forestière, la composition en hôtes et la présence de trouées naturelles. Les résultats ont montré: (*i*) une corrélation significative entre la richesse et la densité des arbres, (*ii*) une diminution de la richesse en fonction du nombre de strates de végétation et (*iii*) une fructification plus importante de certaines espèces près de *Q. ilex* ou d'*Arbutus unedo* L. Une autre caractéristique remarquable était que la richesse et la production étaient plus élevées dans les ouvertures de canopée. Une fructification préférentielle de certaines espèces était aussi observée dans ces ouvertures. Ces résultats mettent en évidence l'importance de la structure forestière et des bois morts de grande dimension pour la conservation in situ des champignons.

Mots clés : communautés ectomycorhiziennes, champignons saprophytiques, chêne vert, patrons de fructification des macromycètes, trouées naturelles, conservation in situ des champignons.

Received 5 January 2004. Published on the NRC Research Press Web site at http://canjbot.nrc.ca on 8 December 2004.

F. Richard[1,2] **and M. Gardes.**[3] Unité mixte de recherche 5174 Évolution et Diversité Biologique, Université Toulouse III Paul Sabatier, 118 Route de Narbonne, 31062 Toulouse CEDEX 4, France.
P.-A. Moreau.[4] Geobotanische Institut ETH, Zollikerstrasse 107, CH 8008 Zürich, Switzerland.
M.-A. Selosse.[3,5] Systématique, adaptation et évolution, Centre national de la recherche scientifique, Université Paris VI, Muséum national d'histoire naturelle, 43, rue Cuvier, 75005 Paris, France.

[1]Corresponding author (e-mail: richard.fran@wanadoo.fr).
[2]Present address: Office National des Forêts, 20250 Corte, France.
[3]These two authors have contributed equally to the supervision of this work.
[4]Present address: Laboratoire de Botanique, Faculté des Sciences Pharmaceutiques et Biologiques, Lille II, 3, rue du Professeur Laguesse, B.P. 83, F-59006 Lille CEDEX, France.
[5]Present address: Centre d'Ecologie Fonctionnelle et Evolutive, Centre National de la Recherche Scientifique, Unité mixte de recherche 5175, Equipe co-évolution, 1919, route de Mende, 34 293 Montpellier CEDEX, France.

 doi: 10.1139/B04-128

Introduction

Old-growth forests are rare in Europe, particularly in the Mediterranean basin, because of ancient anthropic pressures (Quézel and Médail 2003). These forest ecosystems are generally characterised by (*i*) a high diversity of ligneous and herbaceous plants species, (*ii*) numerous old and large trees, and (*iii*) a mosaic pattern of trees at various stages of development. In addition, one of their most noteworthy architectural features is the presence of numerous gaps resulting from tree falls (Oldeman 1990). These small-scale canopy gaps play a key role in natural regeneration of unmanaged forests (Connell 1978; Mc Carthy 2001).

Superimposed on this complex structure, old-growth forests also harbour a high diversity of interacting plants, animals, and fungi (Berglund and Jonsson 2001). Saprobic and ectomycorrhizal (ECM) fungi generally form species-rich guilds that interact with trees (Dahlberg et al. 1997; O'Dell et al. 1999; Smith et al. 2002). Thus, saprobic fungi are primary decomposers of dead organic plant material and ECM fungi develop symbiotic structures, ectomycorrhizae, on fine root tips of numerous tree species (Smith and Read 1997). Identification of the fungi is based almost exclusively on their sexual reproductive structures (commonly referred to as mushrooms, fruitbodies, or sporocarps).

Ectomycorrhizal fungi are taxonomically diverse (>5000 species) and belong to several clades in the Ascomycotina and Basidiomycotina (Smith and Read 1997). A large majority of species produce fruitbodies that are visible above ground, with the naked eye. However, there are ECM fungi (e.g., *Cenococcum geophilum*) for which the sexual stage has not been observed, and others that form inconspicuous fruitbodies (e.g., resupinate *Thelephoraceae* and *Sebacinaceae*, and truffle-like fungi). Most studies of ECM fungal communities are based on fruitbody surveys and on molecular investigations of diversity from mycorrhizal rootlets. Some reports allow a comparison between fruiting patterns and ectomycorrhizae. These two approaches show different and sometimes contrasting results (Gardes and Bruns 1996; Horton and Bruns 2001). For example, species that are well represented in the fruiting record are rare below ground and reciprocally. Despite their limitations, fruitbody surveys are a useful way to assess the presence of species in a stand because many ECM fungi produce fruitbodies that can be easily mapped and identified to the species level. In addition, fruiting patterns still provide valuable tools to forest practitioners interested in the management and conservation of nonwoody resources such as edible mushrooms.

Factors driving fungal diversity remain unclear, but composition and demographic features of the host tree population (i.e., changes in ecosystem structure) are likely to act, particularly on symbiotic fungi (Smith and Read 1997). ECM fungal species differ in their host breadth, ranging from narrow to broad spectra (Molina et al. 1992). Similarly, plants vary widely in their ability to associate with fungal species. As a result, host composition can shape the diversity of the fungal guild (Villeneuve et al. 1989; Nantel and Neumann 1992; Vogt et al. 1992). Fungal richness and composition also change in relation to forest succession (Keizer and Arnolds 1994; Smith et al. 2002). Some ECM species (referred to as early-stage fungi; Last et al. 1987) establish early and stop fruiting in old stands, although they can persist on roots (Smith and Read 1997). During forest maturation, progressive recruitment diversifies the community, introducing species (referred to as late-stage fungi, Last et al. 1987) that often fruit in old stands. Indeed, early-stage fungi with ruderal strategies and late-stage fungi with competitive or stress-selected strategies have been suggested as functional groups (Deacon and Fleming 1992). Further evidence that host demography may be involved in fungal community dynamics is provided by the descriptions of major disturbance effects on diversity. Thus, shifts in the ECM fungal community have been observed following clear-cuts (Jones et al. 2003), volcanic eruptions (Nara et al. 2003), or wild fires (Baar et al. 1999; Dahlberg et al. 2001). Canopy gaps and subsequent regrowth create a diverse age structure of trees, so it is likely that old-growth forests will contain early and late succession ECM fungi. However, to our knowledge, the local effects of natural canopy gaps on fruiting patterns and species richness have not been explored.

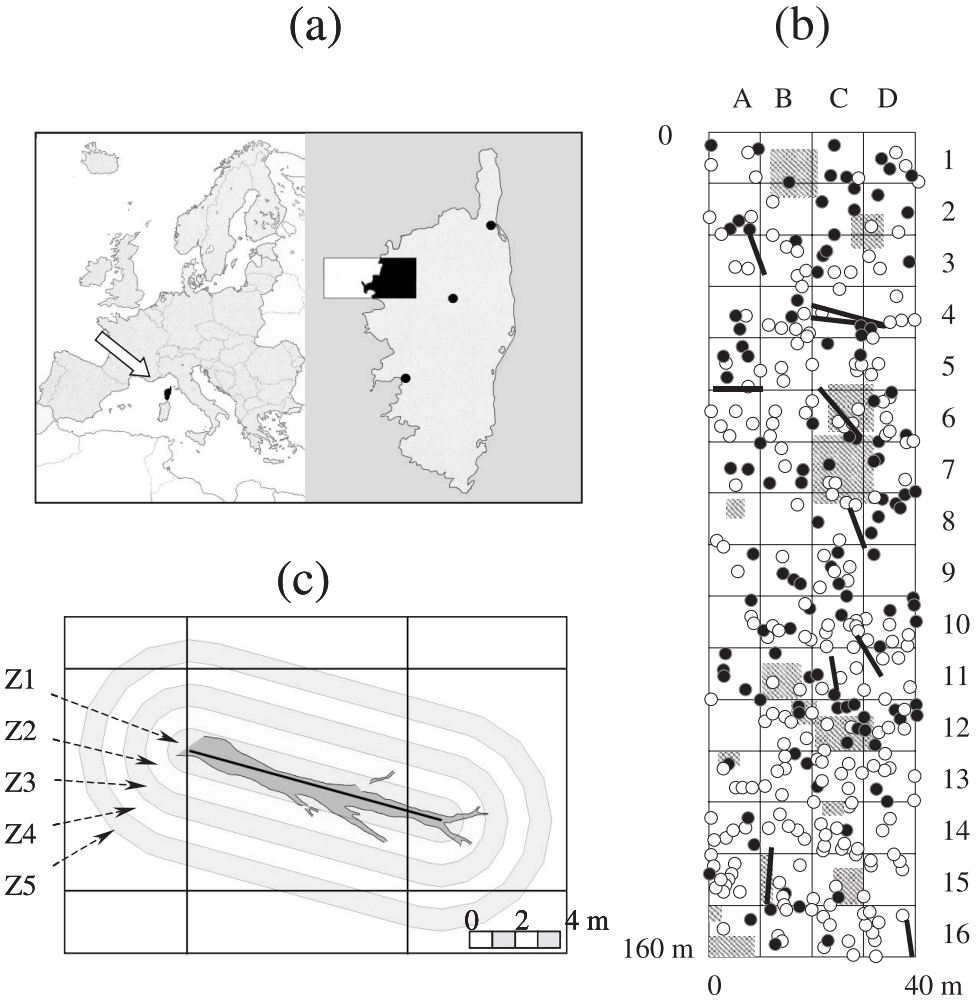
We investigated the fruiting patterns of macromycetes at local scale in an old-growth forest dominated by *Quercus ilex* L. The study was initiated in 1999 within a 6400-m^2 permanent plot located in the Fango forest (Corsica Island). This work opens a new window on Mediterranean diversity, in a climatic region usually described as a diversity hot-spot for many other organisms (Cowling et al. 1996; Médail and Verlaque 1997). In addition, our study plot provides a model in which the role of natural forest dynamics can be tested because plant composition and vegetation structure have been described on a fine scale-grid in a previous study (Panaïotis et al. 1997). Our major objectives were (*i*) to document the ectomycorrhizal diversity in an unmanaged Mediterranean forest ecosystem and (*ii*) to correlate fruiting patterns with host-tree distribution and other forest structural features such as tree density and canopy gaps. We also tested whether the ECM community could be divided in various components, based on host specificity and life history traits of species such as fruitbody size, temporal fruiting patterns, fruitbody abundance, and spatial frequency. In addition to the ectomycorrhizal fungal community, we examined the diversity of saprobic fungi, which are submitted to the same abiotic conditions, but lack any direct connection to living plants.

Materials and methods

Location of the study site and habitat characteristics

The study site is located within the Fango forest (42°20′N; 8°49′E) at the northwestern edge of Corsica Island (Fig. 1*a*). This French island extends between sea level and a maximal altitude of 2710 m. The Fango valley has been a Man and Biosphere (MAB) reserve since 1973, as it contains one of the rare old-growth *Q. ilex* (holm oak) forests of the Mediterranean basin (Quézel and Médail 2003). The Fango forest covers a 4318-ha area on Hercynian granite with enclaves of volcanic rhyolites. It is dominated by sclerophyllous evergreen Mediterranean species, among which *Q. ilex* occurs in the mesomediterranean belt (i.e., between 200 and 900 m above sea level). Soils are alocrisols (AFES 1995) with mull humus overlying (*i*) a thick organic layer with a slightly acidic pH ranging from 5.7 to 6.4 and a

Fig. 1. (*a*) Location of the study site on Corsica Island (France). (*b*) Spatial distribution of the individuals of *Quercus ilex* and *Arbutus unedo* in the study plot (6400 m^2). ●, *Q. ilex* standing trees; ○, *Arbutus unedo* shrubs; lines, *Q. ilex* fallen trees; hatched zones, rocks and screes. (*c*) Concentric zones (Z1–Z5) created using Arcinfo software to analyse the relationship between fruiting patterns and canopy gaps. The grid indicates limits of the 100 m^2 plots.



C to N ratio ranging from 24 to 28 and (*ii*) an altered granite horizon. The climate is subhumid with a mean annual rainfall of 750 mm and an average annual temperature of 14.6 °C at 192 m above sea level. Temperatures range from 3.5 °C (mean January minima) to 29.9 °C (mean July maxima).

Characteristics of the *Q. ilex* old growth stand

The study stand is located in a 15-ha *Q. ilex* old-growth forest that consists of numerous large trees and a 7-m-high dense chaparral. This dense understory layer consisted principally of *Phillyrea latifolia* L., *Erica arborea* L., *Arbutus unedo* L. (strawberry tree) shrubs and other rare species scattered throughout such as *Cistus salviifolius* L. and *Cistus monspeliensis* L. (Gamisans 1999; Panaïotis et al. 1997; data not shown). Of the woody species, only *Q. ilex*, *Arbutus unedo*, and the two species of *Cistus* have the ability to associate with ECM fungi.

The forest shows numerous canopy gaps of about 100 m^2 each (Panaïotis et al. 1995), which occur when old *Q. ilex* stems (170 ± 46 years) break and fall down (Fig. 1*b*). In this paper, natural gap is defined as the surface of the forest floor directly located under the canopy opening, following the terminology of Mc Carthy (2001).

Collecting macrofungi and plants and processing of field data

The fruitbody survey was conducted within a 6400-m^2 (160 m × 40 m) permanent transect that extended from the upper *Q. ilex* forest limit at 390 m down to 330 m (Fig. 1*b*). This transect (established in 1994 by Panaïotis et al. (1997)) was divided into 64 contiguous (10 m × 10 m) plots (labelled from A1 to D16, Fig. 1*b*), each divided into 100 (1 m × 1 m) subplots.

Between 1999 and 2002, epigeous fruitbodies of ECM and saprobic macrofungi fruiting on soil were searched weekly over the whole fruiting season, i.e., from September 15th to March 15th. The position of each fruitbody was recorded and mapped with a 0.1-m resolution using the GIS (Geographical Information System) software Arcview 3.2a (ESRI Inc, Paris). Species forming microscopic, hypogeous, or resupinate fruitbodies were not taken into account. Fruitbodies of parasitic or saprobic species fruiting directly on woody debris, fresh dungs, or living plants were also ig-

nored, as their repartition is obviously determined by the occurrence of such substrates.

Fungal collections were identified to species level in most cases and occasionally to subspecies (= variety) level. Taxa poorly monographed, at least for this Mediterranean region, were ascribed to broad taxonomic units according to Bon (1988) or, alternatively, to unidentified species that were delineated for this study (Appendix A, Tables A1 and A2). Over 3 years, we only removed a minimal number of fruitbodies for identification. Representative voucher collections for all ECM taxa were deposited in the herbarium of the Évolution et diversité biologique laboratory (Unité mixte de recherche 5174, Université Toulouse III Paul Sabatier, Toulouse, France), as were vouchers of 25 saprobic taxa for which identification was doubtful in the field (noted by asterisks in Table A2). In addition, a picture database of saprobic species was prepared and deposited in the same place.

Vascular plants were first recorded in 1994 by Panaïotis and Gamisans (unpublished data). They were surveyed again in 2002, together with nonvascular plant species. *Quercus ilex* and *Arbutus unedo* individuals were mapped at a 0.1-m accuracy, but seedlings were not considered. Large rocks and loose rock debris were also positioned (Fig. 1*b*).

All field data were stored using Arcview 3.2a software.

Assignment of ECM status and diversity analysis

Fungal taxa belonging to genera for which ectomycorrhizae have been undoubtedly reported in the literature were ascribed to the ECM guild (Table A1). We included all genera and species of uncertain ECM abilities (e.g., *Clavulina*, *Clavulinopsis*, *Entoloma*, and *Hygrocybe*) in the saprobic guild (Table A2). Species abundance was calculated as the cumulative number of fruitbodies produced by a given species in the period 1999–2002 (i.e., during three consecutive fruiting seasons; absence or presence data were used because counting fruitbodies (instead of biomass measurements) does not affect fruiting patterns and diversity). Species frequency corresponds to the percentage of spatial units (plots or subplots, depending on the analysis) in which a given species fruited at least once during the entire sampling period (Bills et al. 1986; Villeneuve et al. 1989). Production (also referred to as fruitbody abundance) was defined as the total number of fruitbodies encountered over the period September 1999 – March 2002. Species diversity was estimated using (*i*) richness, that is, the total number of taxa (S; S_m and S_s for ECM and saprobic fungi, respectively), (*ii*) Simpson's diversity index (D), (*iii*) Shannon–Wiener information index (H'), and (*iv*) Fisher's parameter alpha (Fisher et al. 1943). The distribution of relative species abundance was analysed using a rank–abundance curve.

Statistical analyses of spatial patterns

To examine whether differences in community composition arise as a result of geographical distance, we performed a spatial autocorrelation test at the (100 m^2) plot level. We examined the correlation between geographic distance and community similarity among plot pairs. Distances among plots were measured as the distance between plot centers. The similarity matrix was constructed using either Jaccard (J) or Sorensen (S') coefficients that were calculated as follows:

$$[1] \qquad J = c/(a + b - c)$$

$$[2] \qquad S' = 2c/(a + b)$$

where a is the total number of species in one plot, b is the total number of species found in the other plot, and c is the number of species the two plots have in common. Correlation between geographic distance and community similarity was assessed using a Mantel test in the R Package for Multivariate and Spatial Analysis version 4.0 (Casgrain and Legendre 2001; www.fas.umontreal.ca/BIOL/Casgrain). The Mantel's standardized r values range from –1 (negative correlation between similarity matrix and distance matrix) to +1 (positive correlation). The significance level was calculated by randomization of one matrix and calculation of Mantel's r value (Mantel 1967) for each random pairing.

To determine fruitbody distribution patterns (i.e., aggregative, random, or regular), we used the Besag function $L(r)$ (Besag and Diggle 1977), calculated as follows:

$$[3] \qquad L(r) = \sqrt{K(r)/\pi} - r$$

where $K(r)$ is the Ripley function (Ripley 1977) and r is the distance. The function $L(r)$ was calculated for distances that range from 0.5 to 20 m (i.e., half of the transect width) and correspond to aggregate from 1 to 1250 m^2 on average. Confidence intervals at 99% for the null hypothesis of spatial randomness were calculated using the Monte Carlo method using the software ADE-4 (Thioulouse et al. 1997).

The analysis was performed for (*i*) the ECM community, (*ii*) the saprobic community, and (*iii*) species with sample sizes greater than 64 fruitbodies, that is, for those species that could potentially be encountered in all 64 plots of the transect. Calculations were not done for less abundant species because of the inherent lack of statistical power.

Search for correlations between the fungal community and structural characteristics of the forest

First, we examined at the plot level the relations between either fungal productivity or species richness and three parameters of vegetation structure, that is, tree density, coverage, and number of vegetation layers. Fruitbody abundance and species richness were calculated per plot for both ECM and saprobic fungi and compiled over the entire transect. Individuals of *Q. ilex* and *Arbutus unedo* were mapped and counted in each 100 m^2 plot. We distinguished two vegetation entities: chaparral understory and *Q. ilex* cohort sensu stricto. Each entity was further divided into vegetation layers according to plant height. The chaparral was composed of layer 1 (i.e., 1.5- to 5-m-high shrubs) and layer 2 (i.e., 5- to 10-m-high shrubs). In the *Q. ilex* cohort, we distinguished trees ranging from 5 to 10 m in height (layer 1) from trees higher than 10 m (layer 2). A coverage value was estimated for each layer in each plot and expressed as the percentage of the plot covered by this layer. Finally, the relation between the macrofungal community and forest structure was quantified and tested statistically using the Pearson's correlation coefficient.

Second, we examined the relationships between either fungal productivity or species richness and the presence of

Table 1. Estimators of diversity for the ECM and saprobic fungi.

Diversity index	ECM community	Saprobic community
Shannon–Wiener information index (H')		
Using abundance	5.48	4.33
Using frequency	5.98	4.98
Simpson's diversity index (D)		
Using abundance	0.953	0.918
Using frequency	0.975	0.948
Fisher's alpha value (α)	36.51	14.31
Richness (S)	166	68

Q. ilex and *Arbutus unedo* (i.e., the two dominant ECM hosts in our study site). Circular zones (1 or 2 m in radius) centred on *Q. ilex* and *Arbutus unedo* individuals were simulated using Arcview software. Fruitbodies and species of ECM and saprobic fungi were counted in each zone, summed at the plot level, and expressed per square meter per plot. Values were then compiled over the entire study site. Finally, Mann–Whitney nonparametric tests were performed for three distance classes (i.e., 0–1 m; 1–2 m, and 0–2 m) to test for differences in macromycete fruiting patterns between *Q. ilex* and *Arbutus unedo*.

Third, we examined qualitatively and quantitatively the effect of canopy gaps on the fruiting fungal community. Ten canopy gaps were identified over the entire transect based on the presence of fallen *Q. ilex* trunks above the ground. The decaying trunk in each gap was mapped at a 0.1-m accuracy. Five concentric zones (Z1–Z5; 1–5 m in radius) centred on the tree trunk were simulated using Arcview software (Fig. 1*c*). Fruitbody abundances and species richness were calculated at the subplot level in each zone. A Kruskal–Wallis nonparametric test was performed with five distance classes, each corresponding to one of the five zones. This statistical test was done for (*i*) the whole ECM fungal community, (*ii*) the whole saprobic community, (*iii*) abundant species (ECM and saprobic) that produced more than 30 fruitbodies during the period 1999–2002, and (*iv*) saprobic species known to have some wood-decaying abilities such as *Armillaria mellea* (Vahl: Fr.) Kumm..

Classification of ECM taxa based on life history traits

We documented seven life history traits for each of the 128 well-identified ECM species or subspecies (Table A1). Three traits were caused by temporal variation in fruitbody production: (*i*) duration (days) of the fruiting period, (*ii*) periodicity (number of days between the production peak and the beginning of the fruiting season), and (*iii*) fluctuation from one year to another. The last four traits included (1) abundance (number of fruitbodies per 100 m^2 plot), (2) spatial frequency (i.e., number of 100 m^2 plots in which a species is present), (3) mean diameter of the fruitbody cap, and (4) host range. Traits 3 and 4 were documented using compiled litterature from Bon (1988) and P.-A. Moreau's unpublished data for rare species. A multivariate Hill and Smith analysis (Hill and Smith 1976) was performed on qualitative and quantitative traits using the software package ADE-4 (Thioulouse et al. 1997). The Ward's linkage method based on Euclidian distances (Ward 1963) was then used to define groups of taxa. Their significance was assessed using a random permutation test with 1000 permutations (Manly 1997). Finally, using Mann–Whitney nonparametric tests we investigated the relationship among the life history traits that we identified as being discriminating using results from the multivariate analysis.

Results

Diversity of the macrofungal communities

As a result of 78 weekly surveys over three consecutive fruiting seasons (in the period 1999–2002), we recorded 5382 fruitbodies of macromycetes. A total of 234 species were found, including 166 ECM taxa (S_m) and 68 taxa (S_s) of saprobic fungi (Table 1). In contrast, only 19 angiosperm species were collected out of 36 Embryophytes (data not shown). In addition to this low plant diversity, the vegetation survey showed that the ECM plants at our site consisted only of *Q. ilex* and *Arbutus unedo*, with the exception of two small individuals of *Cistus*.

The ECM fungal community was represented by 25 genera of Basidiomycetes (22) and Ascomycetes (3), out of 3659 collected fruitbodies (Fig. 2*a*). Members in the family *Russulaceae* accounted for 40.5% of the fruitbodies and 31.9% of the taxonomic diversity. At the genus level, three main patterns were observed: (*i*) species-rich and highly productive genera, e.g., *Russula* and *Amanita*, (*ii*) species-rich but unproductive genera, e.g., *Tricholoma* and *Cortinarius* (23.5% of S_m and 6.7% of the ECM fruitbody production); and (*iii*) species-poor but highly productive genera, e.g., *Lactarius* and *Hydnum* (Fig. 2*a*). The ECM community was also strongly dominated by rare species with more than 60.8% of the taxa (101 out of 166) producing less than 1 fruitbody per 1000 m^2 on average (Fig. 3, Table A1). At the other extreme of the rank–abundance curve, the three dominant species, *Laccaria laccata* (Scop.: Fr.) Berk. & Broome, *Lactarius chrysorrheus* Fr, and *Inocybe tigrina* R. Heim, produced 32.9% of all fruitbodies (Fig. 3, Table A1).

The saprobic taxa were distributed over 31 genera of Basidiomycetes (28) and Ascomycetes (3), out of 1723 collected fruitbodies (Fig. 2*b*). The community was mainly composed of *Marasmiaceae* (44.7% of the total fruitbody number). The two most abundant species were *Mycena vitilis* (Fr.) Quél. and *Lycoperdon perlatum* Pers.: Pers., which together produced 30% of saprobic species fruitbodies. As for ECM fungi, rare taxa also dominated this community since 58.8% of taxa (40 out of 68) produced less than 1 fruitbody per 1000 m^2 on average (Fig. 3, Table A2).

The Shannon–Wiener information index (H'), the Simpson's diversity index (D), and the Fisher's alpha value were high (relative to other diversity studies) using either

Fig. 2. Relative abundance of fruitbodies (filled bars) and relative species diversity (open bars) of the most abundant genera for ECM fungi (*a*) and saprobic fungi (*b*).

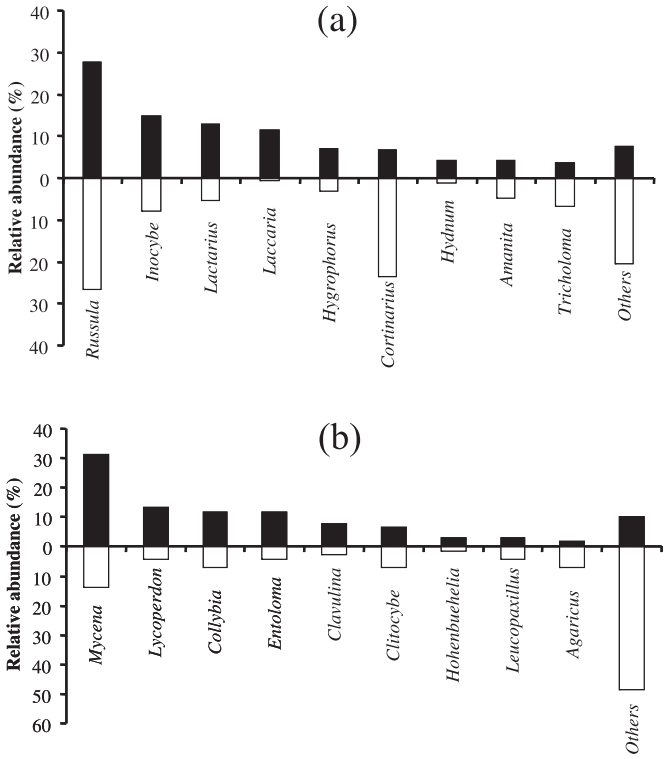
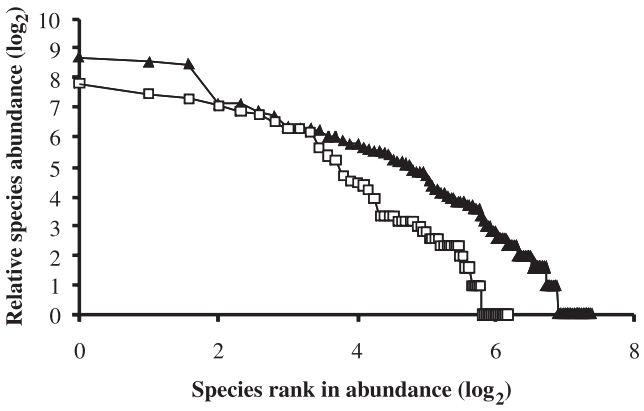


Fig. 3. Dominance–diversity curves for ECM (▲) and saprobic (□) taxa of macrofungi. Most frequent species to least frequent ones are ordered from left to right.



fruitbody abundance or frequency (Table 1). They were also greater for ECM than for saprobic fungi.

Spatial patterns of species and fruitbodies

The Mantel's test showed a low r value and a significant autocorrelation at the plot level for ECM fungi, using Jaccard's and Sorensen's coefficients ($r = 0.079$, $p = 0.030$ and $r = 0.076$, $p = 0.047$, respectively). These results suggest that community similarity remains nearly constant as the interplot distance increases. No spatial autocorrelation was found for saprobic fungi ($r = -0.011$, $p = 0.380$ and $r = -0.019$, $p = 0.310$ using Jaccard's and Sorensen's coefficients, respectively).

Fruitbodies were unevenly distributed on the study site. We found a few highly productive plots and numerous unproductive plots. For example, clustered fruiting was observed in two groups of adjacent plots (i.e., A3 + B2 + B3 and A7 + B7, Fig. 1*b*) that harboured 18% of the ECM fruitbody production (i.e., twice the expected number of fruitbodies in an assumed uniform area of the same size). These plots were also species-rich since they included 66% of the taxa (i.e., 2.4 times the expected number). In contrast, four groups of plots (i.e., C1 + D1 + D2 + D3 + D4, C7 + D7, A8 + B8 + D8, and D11, Fig. 1*b*) covering 1100 m^2 (17.2% of the transect) exhibited only 5.1% of the total ECM fruitbody production (three times less than the mean production). Such unproductive plots were generally species-poor and typically contained 6–8 ECM taxa (data not shown); they were mainly observed in zones with screes at ground level. For saprobic fungi, three plots (i.e., C4, B7, and A12, Fig. 1*b*) covering 4.7% of the total area exhibited 28.8% of the fruitbody production while 32 others (50% of the total area) accounted for only 10.8% of the production.

Rare species were evenly encountered in the 6400 m^2 *Q. ilex* stand. They were scattered in 87.5% (56 out of 64) and 62.5% (40 out of 64) of the 100 m^2 plots for ECM and saprobic species, respectively (data not shown). In contrast, abundant species (i.e., those that produced more than 64 fruitbodies over 3 years) were not regularly distributed. Of the 12 abundant ECM species, nine occurred in half of the 100 m^2 plots or more, but none fruited in all plots (Table A1, column 4). As revealed by the Besag function, the distribution of fruitbodies of these abundant species was mainly aggregative with the exception of two ECM taxa, *Russula delica* and *Russula olivacea*, and two saprobic fungi, *Mycena vitilis* and *Mycena alcalina* (Table 2). The ECM aggregates ranged from 20 m^2 for *Laccaria laccata* to 200 m^2 for *Russula fragilis*. At the community level, aggregates were also found consistently each year, except year 2 for saprobic fungi (Table 2). ECM aggregates covered a 12- to 50-m^2 area in average.

Production and species richness in relation to vegetation coverage, number of layers, and ECM host density

Negative correlations were found between the fungal community and the number of vegetation layers (with the exception of saprobic production) (Table 3). These results suggest that the fruiting fungal community may respond to canopy closure. In addition, ECM richness was negatively correlated to *Q. ilex* density but positively correlated to *Arbutus unedo* density (Table 3), suggesting a potential (but distinct) role of these two ECM hosts on fungal diversity. A similar pattern was also observed for the saprobic fungi as richness was negatively correlated to *Q. ilex* density and coverage (Table 3). A negative correlation was also found between production of saprobic fungi and total vegetation coverage.

Production and species richness in relation to the presence of *Q. ilex* and *Arbutus unedo*

No significant difference was observed in ECM species richness and fruitbody abundance between *Arbutus unedo*

Table 2. Spatial patterns of fruitbodies using the Besag function (Besag and Diggle 1977).

	Aggregative spatial pattern	Random spatial pattern
Whole community		
Ectomycorrhizal	Season 1 (12), 2 (27), 3 (50 and 710), and all three seasons (50)	
Saprobic	Season 1 (50), 3 (50 and 615), and all three seasons (no clear scale)	Season 2
Abundant taxa		
Ectomycorrhizal	*Laccaria laccata* (20), *Lactarius chrysorrheus* (50), *Inocybe tigrina* (20), *Hydnum repandum* (150), *Russula acrifolia* (30), *Hygrophorus russula* (50), *Russula risigallina* (30), *Russula fragilis* (200), *Tricholoma saponaceum* (80), *Cortinarius elatior* (50)	*Russula olivacea*, *Russula delica*
Saprobic	*Lycoperdon perlatum* (250), *Entoloma nidorosum* (400), *Clavulina cinerea* (590), *Collybia butyracea* (200), *Clitocybe gibba* (no clear scale), *Collybia dryophila* (10), *Mycena pura* (250)	*Mycena vitilis*, *Mycena alcalina*

Note: The size (in square meters) of aggregates is given in parentheses.

and *Q. ilex* (Table 4). However, some ECM species fruited preferentially (significant differences by Mann–Whitney nonparametric tests) either near *Q. ilex* (e.g., *Russula decipiens*, *Russula acrifolia*, and *Sarcodon cyrneus*), or near *Arbutus unedo* (e.g., *Inocybe geophylla* var. *lilacina*, *Leccinum corsicum*, *Tricholoma ustale*, and representatives of the genus *Inocybe*) (data not shown). In addition, taxa such as *Leccinum corsicum* or *Inocybe cervicolor* were always absent from *Q. ilex* stem vicinity.

In contrast to ECM fungi, a clear distinction was observed for saprobic fungi between these two woody plants. Fruitbody abundance was higher near *Arbutus unedo* shrubs (within the first 2 m) than near *Q. ilex* trees (Table 4). Species were also more numerous (Table 4). Many of them such as *Calocybe carnea*, *Clavulina cinerea*, and *Clitocybe odorata* tended to fruit more frequently close to *Arbutus unedo* than in other areas (data not shown).

Production and species diversity in relation to the presence of canopy gaps

Fruiting patterns were analysed at various distances (zones Z1–Z5, Fig. 1*c*) from fallen *Q. ilex* trunks. In Z1, ECM fruitbody production and species richness were respectively 27% and 31% higher than outside gaps (Fig. 4*a*). Species richness and production were also significantly enhanced for saprobic fungi in Z1, i.e., within the first meter around the dead trunk (Fig. 4*b*). In the four following meters (from Z2 to Z5), values decreased drastically for both ecological groups, suggesting a strong and localized effect in the nearby proximity of the decaying trunk. Thus, the ECM community was 42% less productive in Z4 and 40% less diverse in Z5 than it was outside gap (at >5 m away; Fig. 4*a*).

At the species level, differences in fruitbody production were also detected between gap and non-gap areas (Table 5). Some ECM species were highly productive in gaps, others were absent or rarely encountered. For example, *Russula vesca*, *Russula persicina* var. *rubrata*, and *Lactarius rubrocinctus* produced two to nine times more fruitbodies in Z1 than in the non-gap area. In contrast, another set of abundant taxa (e.g., *Laccaria laccata*, *Russula chloroides*, and *Inocybe geophylla*) and species of the genus *Hebeloma* were absent or weakly represented in gaps. A similar pattern was observed for saprobic species. Production of well-known wood-decaying species such as *Armillaria mellea*, *Leucopaxillus gentianeus*, and *Leucopaxillus tricolor* was particu-

Fig. 4. Fruitbody production (top bars) and species diversity (bottom bars) of macrofungi in canopy gaps versus closed canopy forest (>5 m from fallen trunk) at the subplot level. (*a*) ECM species. (*b*) Saprobic species. Means followed by the same letter do not differ significantly at the 5% level. Error bars are standard deviations.

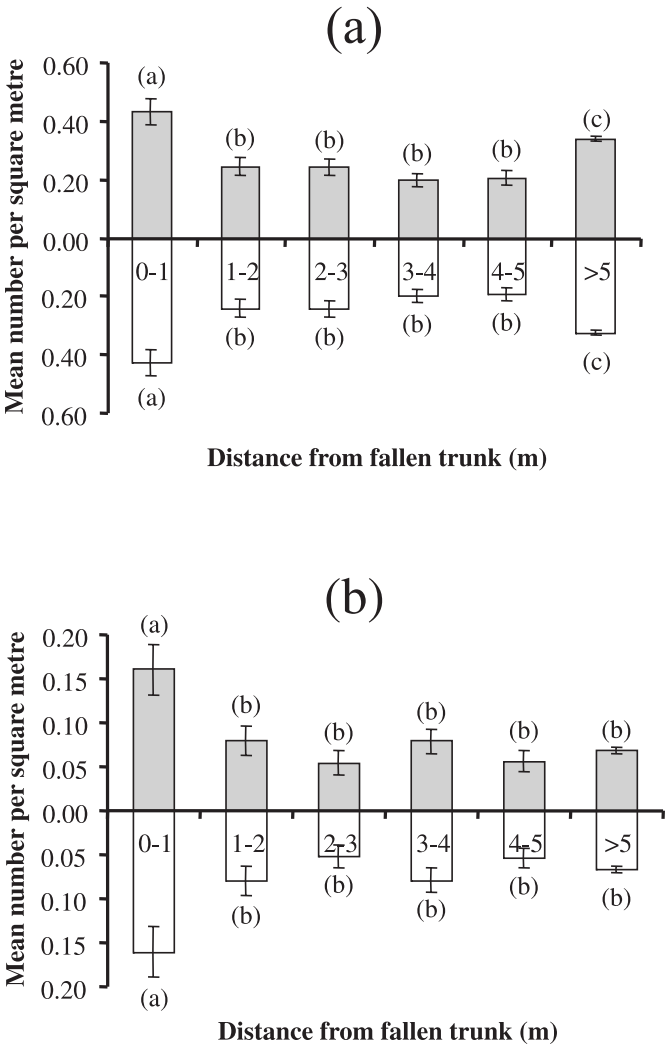


Table 3. Relationships between the fruiting fungal community and forest structure including *Quercus ilex* and *Arbutus unedo* density and coverage, and number of layers.

	ECM fungi		Saprobic fungi		All macrofungi	
	Production	Richness	Production	Richness	Production	Richness
Q. ilex density*	–0.134 (0.290)	–0.298‡ (0.017)	0.202 (0.109)	–0.340‡ (0.006)	–0.215 (0.088)	–0.350‡ (0.005)
Arbutus unedo density*	0.139 (0.274)	0.244‡ (0.050)	–0.122 (0.336)	0.075 (0.554)	0.004 (0.978)	0.213 (0.091)
Q. ilex coverage	–0.153 (0.226)	–0.234 (0.063)	–0.182 (0.151)	–0.342‡ (0.006)	–0.213 (0.091)	–0.302‡ (0.015)
Chaparral coverage	0.049 (0.698)	0.216 (0.087)	–0.078 (0.543)	0.233 (0.064)	–0.021 (0.868)	0.249‡ (0.047)
(*Q. ilex* + chaparral) coverage	–0.083 (0.515)	0.033 (0.796)	–0.252‡ (0.044)	–0.045 (0.724)	–0.217 (0.085)	0.009 (0.946)
Total number of layers†	–0.254‡ (0.043)	–0.298‡ (0.017)	–0.237 (0.059)	–0.453§ (0.000)	–0.311‡ (0.012)	–0.298§ (0.001)

Note: Quantification of the relationships was performed using Pearson's correlations coefficients at the plot level. Probability (p) values are given in parentheses.
*Density was defined as the number of *Q. ilex* or *Arbutus unedo* individuals per 100 m^2 plot.
†For each vegetation entity, we only considered layers that represented at least 10% coverage.
‡Significant correlation at $p < 0.05$.
§Significant correlation at $p < 0.001$.

larly important in gaps (Table 5). For example, 25 out of 26 *Armillaria mellea* fruitbodies were collected in Z1, and 41 out of 42 *Leucopaxillus gentianeus* fruitbodies occurred in Z1, Z2, and Z3 (data not shown). Conversely, despite its abundance (Table A2), the litter-decaying species *Collybia butyracea* was rarely found in gaps, and never in the first three zones (Table 5).

Grouping of ECM fungi based on host specificity and life-history traits

The ECM community included species reported to associate with (*i*) a large range of angiosperms (e.g., *Scleroderma verrucosum* and *Russula amoenicolor*), (*ii*) trees in the family *Fagaceae* (e.g., *Russula grisea*), and (*iii*) various species of oaks (e.g., *Lactarius chrysorrheus* and *Hygrophorus russula*) (Table A1). It also included broad host range species (e.g., *Laccaria laccata* and *Amanita phalloides*) reported to associate with both Angiosperms and Gymnosperms. Furthermore, the community contained a small group of species restricted to Mediterranean *Q. ilex* forests (11 taxa, e.g., *Russula laricino-affinis* and *Sarcodon cyrneus*), chaparrals (5 taxa, e.g., *Russula cistoadelpha* and *Amanita gioisa*), or other thermophilic angiosperm forests (17 taxa, e.g., *Boletus aereus* and *Cortinarius caligatus*). This entire group of habitat-restricted species encompassed 25.9% of the species richness and 9.9% of the fruitbody production.

Out of 128 identified taxa, 3 (i.e., *Laccaria laccata*, *Inocybe tigrina*, and *Lactarius chrysorrheus*) were clearly separated from the others based on a Hill and Smith multivariate analysis (data not shown). These three species (group A, Table A1) were very abundant in the stand. We excluded them from a second multivariate analysis aiming to separate the remnant species. In this new analysis, the first two factorial axes accounted for 22.2% (F1) and 10.8% (F2) of the total variability, respectively. Two groups of traits appeared to be opposed along the F1 axis: high abundance, high frequency, regular fruitbody production from one year to another, and broad host range (positive scores) versus low abundance, low frequency, high fluctuation in fruitbody production from one year to another, and narrow host range (negative scores) (Figs. 5*a* and 5*b*). The F2 axis further separated thermophilic and chaparral linked species from species with other ecological specificity. The other axes did not add further information (Eigenvalues < 9%, data not shown). Among the 125 ECM taxa, five new groups (B to F) were distinguished using the Ward's method (Fig. 5*c*, Table A1). Random permutation tests performed on these groups showed that within-group inertia was significantly higher than between-group inertia ($p < 0.001$). Groups B, C, and D (92 taxa) were dominated by species that (*i*) were mainly broad host range, (*ii*) fruited regularly (i.e., observed in either 2 or 3 years), and (*iii*) produced a large number of fruitbodies. In contrast, groups E (mainly chaparral restricted) and F (mainly *Q. ilex* linked or thermophilic) encompassed 33 species mainly linked to Mediterranean hosts and producing episodically a few fruitbodies (Table A1). Mann–Whitney nonparametric tests (including all groups, from A to F) confirmed that thermophilic species as well as those frequently encountered in *Q. ilex* forest or in chaparrals (Table A1) had distinctive characteristics. They pro-

Table 4. Production and species richness at various distances from individuals of *Quercus ilex* (n = 108) and *Arbutus unedo* (n = 227).

	0–1 m from tree		0–2 m from tree		1–2 m from tree	
	Q. ilex	*A. unedo*	*Q. ilex*	*A. unedo*	*Q. ilex*	*A. unedo*
ECM fungi						
Production	0.379±0.064a	0.477±0.071a	0.396±0.049a	0.427±0.039a	0.415±0.060a	0.409±0.037a
Richness	0.242±0.039a	0.248±0.027a	0.218±0.022a	0.210±0.015a	0.236±0.027a	0.224±0.018a
Saprobic fungi						
Production	0.117±0.063a	0.187±0.088a	0.069±0.021a	0.202±0.045b	0.045±0.010a	0.210±0.051b
Richness	0.047±0.011a	0.071±0.018a	0.037±0.006a	0.059±0.008b	0.032±0.007a	0.059±0.007b

Note: Numbers are means per square meter at plot level ± SD (n = 64). For each of three distance classes, values followed by different letters indicate a significant difference based on Mann–Whitney nonparametric tests ($p < 0.05$).

Table 5. Mean numbers of fruitbodies per 100 m^2 in gaps (n = 10) and the closed canopy forest for the most abundant ECM and saprobic species.

	Distance from fallen trunk in canopy gaps					
Species	Z1 (0–1 m)	Z2 (1–2 m)	Z3 (2–3 m)	Z4 (3–4 m)	Z5 (4–5 m)	Closed canopy forest (>5 m)
ECM species						
Inocybe tigrina	10.09	12.9	6.97	2.45	7.26	4.84
Russula vesca	2.29*	0.72	0	0	0.24	0.23
Russula persicina var. *rubrata*	1.38	1.79*	0.61	0	0.97	0.46
Russula globispora	1.83	0.71	0.61	0.54	0.24	0.71
Russula fragilis	2.29	1.43	0.61	0.27*	0.48	1.38
Cortinarius elatior	1.83	0.36	0	1.09	0.97	1.11
Lactarius rubrocinctus	1.83	1.08	0.91	0.27	0	0.61
Laccaria laccata	0.46	1.43	2.12	1.36	0.97	7.58
Russula chloroides	0	0	1.21	0.27	0	1.23
Inocybe geophylla	0	0.36	0.91	0.27	0.48	1.06
Whole genus *Hebeloma*	0.46	0	0	0	0	0.63
Saprobic species						
Armillaria mellea	11.47*	0	0	0	0	0.02
Leucopaxillus gentianeus	1.38	0.36	10.3*	0	0	0.02
Leucopaxillus tricolor	1.83*	0	0	0	0	0.02
Collybia butyracea	0	0	0	0.82	0	1.86

Note: Five distance classes corresponding to the five concentric zones in Fig. 1*c* were identified in canopy gaps. They range from 0 to 5 m from the fallen trunk in each gap.

*Significantly different according to Kruskal–Wallis nonparametric tests at $p < 0.05$.

duced significantly fewer fruitbodies (p = 0.011), less frequently (p = 0.007), and less regularly (p = 0.003) than species that are not restricted to a Mediterranean habitat (Table A1). They also had a shorter fruiting period (p = 0.014). No additional difference was found between these two groups of species in fruitbody size or in other phenological characteristics.

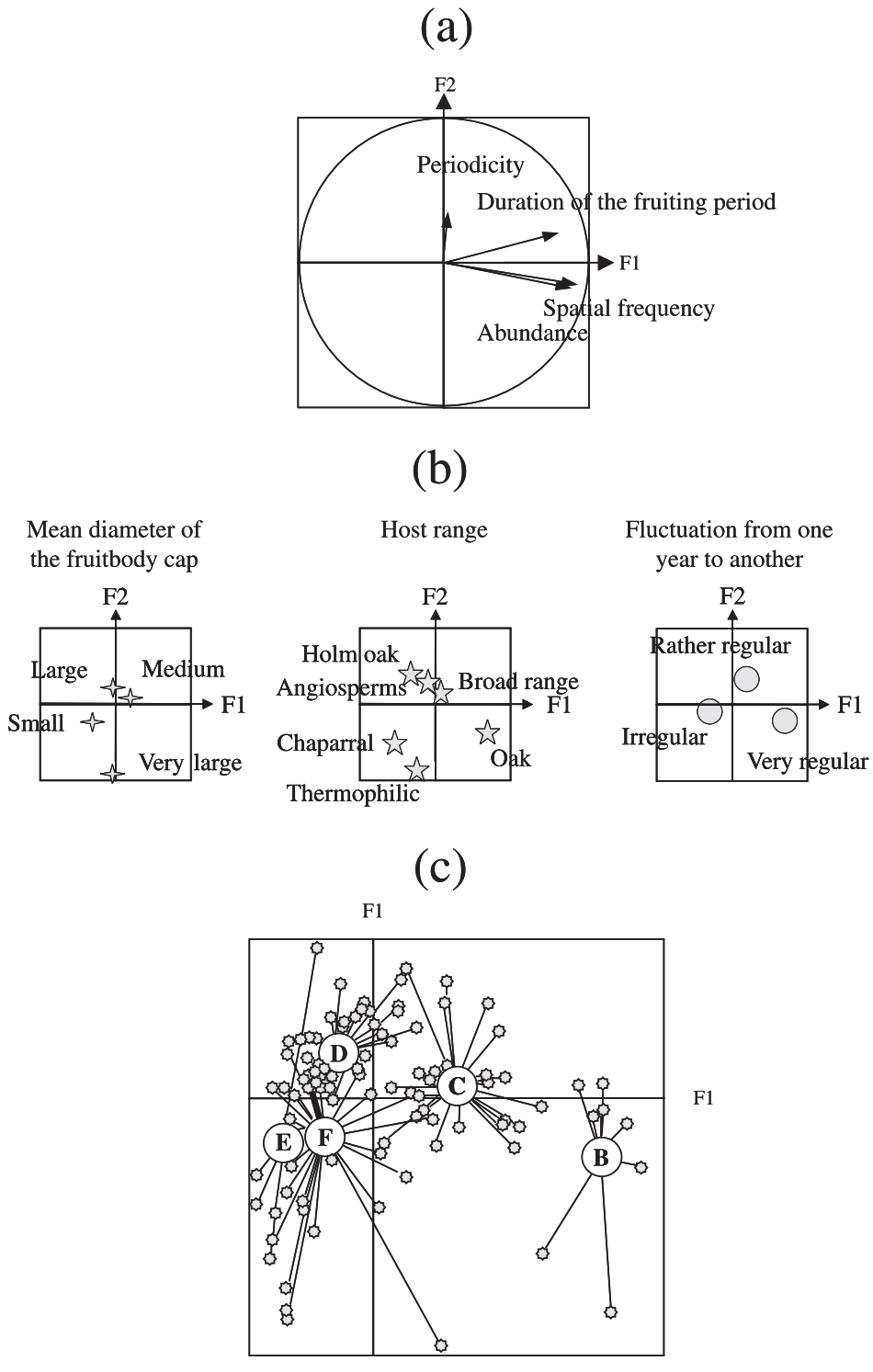
Discussion

ECM richness, fruitbody productivity, and species composition

Only a few studies have dealt with fungal diversity associated with *Q. ilex* (Signorello 1996; Laganà et al. 1999) but none of them in old-growth forests. Our results show that estimates of taxonomic diversity in *Q. ilex* old-growth forests are likely to be tremendously high, especially when considering the large number of rare species found at our site (61.4% of the ECM community), the limited size of our sampling site (6400 m^2), and the limited duration of our survey (3 consecutive fruiting seasons). Thus, species richness was high (S = 166; Table 1) with respect to the low number of ectomycorrhizal hosts and the low productivity of the fungal community during the survey period. However, this value is consistent with others reported from old-growth conifer forests. For example, O'Dell et al. (1999) and Smith et al. (2002) found 150 and 133 ECM species in Douglas-fir (*Pseudotsuga menziesii* Mirb.) and Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stands of similar sizes, respectively. Furthermore, in a comparison of Norway spruce (*Picea abies* L.) forests of different ages, the highest ECM fungal diversity was observed in the oldest, 200-year-old stand (Peter et al. 2001).

In our stand, two ECM hosts (i.e., *Q. ilex* and *Arbutus unedo*) shared 166 fungal symbionts, without taking into account either hypogeous or resupinate taxa, such as

Fig. 5. Hill and Smith (1976) multivariate analysis. (*a*) Correlation circle for quantitative variables. (*b*) Position of modalities for qualitative variables. (*c*) Distribution of species groups.



Thelephoraceae and *Sebacinaceae*. The ECM fungal community was 4.6 times more diverse than the whole plant community, including nonvascular plants (data not shown). Most reported ratios from other forests are lower. They generally range from 0.2 to 1.8 ECM species per vascular plant species (e.g., in deciduous forests dominated by alder (Brunner et al. 1992), oak (Schmit et al. 1999), or birch (Villeneuve et al. 1989)). However, Dahlberg et al. (1997) found a ratio of 3.7 in an old-growth Norway spruce forest. Various factors could account for such a high ratio in our stand: (*i*) historical legacy of ECM fungal diversity and (*ii*) extreme abiotic factors or strong environmental fluctuations leading to species-rich assemblages (Whittaker 1972; Huisman and Weissing 1999). For example, in a study of

hypogeous and epigeous Gasteromycetes from different sites in the Sonora region, a surprisingly high diversity was found in the tropical thorn forest, an extremely xeric habitat, 88.6% of which was covered by a single plant species (Esqueda-Valle et al. 2000). Additional factors could also drive such a diversity at local scale by limiting competitive exclusion among fungal species; they include unrecognized limiting factors or environmental heterogeneities (Tilman 1992) and antagonistic interactions (Czárán et al. 2002). Later on, we discuss environmental heterogeneities in fruiting patterns linked to forest structure and composition.

Another noteworthy feature was the low fruitbody productivity of the ECM community (a feature also shared by saprobic species) (Fig. 3). Most ECM species were represented by less than 1 fruitbody per 1000 m^2 (Table A1). This low productivity together with the high species diversity lead to particularly high values of diversity indexes (Table 1). Similarly, Bills et al. (1986) and Villeneuve et al. (1989) obtained high Shannon's entropy values (ranging from 4.1 to 5.0) for the ECM fruiting community from old hardwood stands. Peter et al. (2001) also reported a high Simpson's index value (0.95) in a 200-year-old Norway spruce forest. Finally, Smith et al. (2002) demonstrated that old-growth Douglas-fir stands were as diverse as young forest with closed canopy, but six times less productive.

The ECM community in our *Q. ilex* stand was very similar to that described by Skirgiello (1998) in another European old-growth hardwood forest in Białowieża (Poland). Striking similarities included (*i*) the high number of species of *Russula* and *Cortinarius*, (*ii*) the low productivity of most *Cortinarius* species, and (*iii*) the high abundance of *Laccaria laccata*. In our stand, species of *Russula* and *Cortinarius* accounted for 50% of the taxonomic diversity (Fig. 2*a*). Species of *Cortinarius* represented only 6.7% of the total ECM fruitbody production (Fig. 2*a*) and *Laccaria laccata* was one of three most abundant producers (Table A1). Similar trends in species composition have been observed in conifer forests. For example, the genera *Russula*, *Cortinarius*, and *Inocybe* accounted for 49% of fruitbody collections and about 52% of taxonomic diversity in an old-growth stand of Douglas-fir (Smith et al. 2002). However, our results differ from other studies undertaken in coniferous dominated old-growth stands, in which species of *Cortinarius* were the most abundant producers, but neither species of *Russula* nor other taxa were abundant (Dahlberg et al. 1997; Peter et al. 2001). In our forest, the genus *Russula* alone represented more than 25% of the number of fruitbodies and species diversity. In summary, the genera *Russula* and *Cortinarius* often dominate most fruiting ECM communities. This result may be explained because fruitbodies of these fungi are usually easy to detect in the field and because these two genera also encompass a very large array of species with diverse ecological requirements. The predominance of *Russula* in a deciduous sclerophyllous forest is interesting although this result requires additional investigations to confirm that *Russula* spp. also dominate the nonfruiting ECM community in the northern hemisphere.

Several life-history traits allowed us to separate the ECM community into six distinct components that a posteriori appeared to differ mainly by fruitbody abundance and host specificity (Table A1). Two striking results emerged from this classification: (*i*) in this Mediterranean forest, the ECM diversity essentially encompassed broad host range species with temperate affinities and (*ii*) a weak Mediterranean component was composed of species that fruited less regularly and less abundantly than temperate taxa. Nearly 90% of fruitbodies were produced by temperate fungal species. A similar trend was already reported by Norstedt et al. (2001) in a polypore survey in endemic Corsican pine forests. More than 56% of species were also encountered in northern Europe. The abundance of species with large geographical distribution may be explained by long-distance fungal dispersal and (or) historical legacies. Alternatively, taxonomic and methodological limitations may bias our view of the fungal diversity and thus the ratio between Mediterranean and temperate fungal taxa. Much of the fungal diversity remains to be described (Hawksworth 2001) and many cosmopolitan taxa may in fact cover several cryptic species, including some restricted to the Mediterranean region. Finally, Mediterranean species may have an erratic fruiting pattern that does not reflect their true diversity and abundance in soil and on tree roots. Thus, as mentioned earlier, below ground communities (i.e., those observed from mycorrhizae and mycelia in the soil) would have to be explored to obtain a comprehensive overview of the ECM community.

ECM versus saprobic fungi

Overall, the ECM fungi appear 2.4 times more diverse and 2.1 times more productive than saprobes. This lack of diversity and productivity in decomposers species is surprising since accumulation of favourable substrates is likely to occur in an old-growth forest (Ohlson et al. 1997). This result may be explained by (*i*) our limited sampling of the decomposer community that excludes wood-decaying fungi, (*ii*) differential responses to dry environmental conditions between ECM fungi and saprobes, and (or) (*iii*) the relatively low C/N ratio of the organic layer (ranging from 24 to 28; data not shown) that would favour ECM fungi but not decomposers.

Spatial distribution of fruitbodies and species

At both the community and species level, we observed aggregative distributions of ECM fruitbodies on areas of various sizes (Table 2). This has been described in a few studies addressing the spatial distribution of epigeous and hypogeous ECM species (Fogel 1976; Yamada and Katsuya 2001). For example, Yamada and Katsuya (2001) reported an uneven distribution of fruitbodies for the most abundant epigeous ECM species in *Pinus densifolia* reforested stands. The presence of fruitbody aggregates among ECM fungi may be indicative of a higher local activity of mycelia and mycorrhizae in relation to soil heterogeneity and (or) host root distribution. As a comparison, the saprobic community did not show scales of fruitbody aggregation as clear as those observed for ECM fungi (Table 2), suggesting differences in fruiting determinism between these two ecological fungal groups and (or) differences in the spatial distribution of mycelia.

A significant spatial autocorrelation was found among ECM taxa using Mantel's test, but it was lower than values obtained in other studies of fruiting ECM communities

(Schmit et al. 1999; Peter et al. 2001). Thus, community composition did not drift away with distance. This can be explained by the large number of rare species with a high spatial equitability (Crawley 1997). Overall, our results entail methodological considerations with regard to the best sampling strategy as follows: (*i*) new species appear slowly as the sampled area increases, (*ii*) spreading out sampling plots is unlikely to increase the capturing of rare ECM species, and (*iii*) sampling few adjacent and productive plots may be as effective as sampling discontinuous heterogeneous areas to characterize most of the fruiting ECM community. These recommendations are applicable to a lesser extent to saprobic fungi as they did not show any significant spatial autocorrelation and species appeared somewhat less clustered than ECM fungi on average (Table 2).

Fungal diversity and productivity in relation to forest structure and composition

Diversity and productivity of the ECM fruiting community decreased significantly as the number of forest layers increased (Table 3). This response is similar to the well-known canopy closure effect on fruiting (Jansen and de Nie 1988; Vogt et al. 1992). In addition, species diversity was influenced by tree and shrub density (Table 3). Species diversity decreased as the number of *Q. ilex* trees increased and was positively correlated to the density of *Arbutus unedo* shrubs. In addition, some species in the ECM community were preferentially encountered near *Q. ilex* or near *Arbutus unedo* (data not shown). We concluded that ECM diversity and productivity are pro parte shaped by the ECM host and forest structure, as already shown by Nantel and Neumann (1992) and Såstad (1995) using fruitbodies, and by Kernaghan et al. (2003) on ectomycorrhizae. No further correlation was found between ECM fruiting patterns and other vegetation descriptors (Tables 3 and 4).

As observed for ECM species, fruiting patterns of saprobic species were sensitive to changes in vegetation structure and composition (Tables 3 and 4). They were highly diverse and abundant under chaparral canopy and decreased drastically as number and coverage of *Q. ilex* increased, suggesting a possible response of these fungi to litter quality.

Role of natural canopy gaps on fungal diversity and productivity

Our results show a strong and localized effect of gaps on fruiting (Fig. 4; Table 5) for both symbiotic and saprobic guilds. ECM fruiting was higher quantitatively (+27%) and qualitatively (+31%) near the decaying tree trunks (Fig. 4*a*). A similar pattern was detected for saprobic fungi with wood-decay abilities (Table 5, Fig. 4*b*). We also found that some ECM species (e.g., the early-stage *Laccaria laccata*) were poor producers in gaps, while six species belonging to late-stage ECM genera (*Russula*, *Lactarius*, and *Cortinarius*) were consistently very abundant within the first meter around the fallen *Q. ilex* trunk (Table 5). These later species might have the ability to acquire carbon from large woody debris in addition to photosynthates from their living hosts. Interestingly, abundant litter decomposers such as *Collybia butyracea* were always found outside the gaps in contrast to several saprobic species with wood decaying abilities (Table 5). Alternative explanations to the observed diversity patterns in gaps include shifts in abiotic conditions. Thus, light level on the forest floor is known to increase with canopy opening, including in small gaps (Chazdon and Fetcher 1984; Canham et al. 1990). This, in turn, affects soil temperature, soil nutrients, and soil moisture (Mehus 1986; Mc Carthy 2001). These changes in abiotic conditions have the potential to drive the physiological and metabolic activities of the fungal symbionts and, as a result, the diversity and productivity of the entire fruiting community. Regardless of the mechanisms involved, our results highlight the role of canopy gaps as favourable habitats for ECM fungi in an old-growth sclerophyllous forest. Moreover, these results confirm the primary importance of large woody debris for the conservation and management of the fungal diversity in *Q. ilex* forests, as shown in other ecosystems (Harvey et al. 1978; Goodman and Trofymov 1998; Tedersoo et al. 2003).

Conclusions and perspectives

Our sampling protocol was aimed at producing a fair image of a local macromycete fruiting community in terms of taxonomic composition. Results suggest that Mediterranean old-growth forests are of great interest for conservation of the species diversity of ECM fungi, as shown by the unusual high richness and diversity of the fruiting community in our 6400-m^2 study site. The paradox of a few tree species associated with a large array of ECM fungal species, already described in temperate ecosystems (Malloch et al. 1980), applies to Mediterranean ecosystems, but we also found evidence of a partial determinism of forest structure and host dynamics in building various niches, mainly through gaps created by fallen trees. Future work will include a description of below ground communities to obtain a more comprehensive view of the diversity. Comparisons with other sites should also be attempted on the basis of parameters such as Fisher's alpha index or the species accumulation curve. Further investigations are required to understand mechanisms affecting the diversity and fruiting of fungal species. Another intriguing question is the ecological role of this ECM diversity and its possible feedback on host tree dynamics.

Acknowledgements

This study is part of F. Richard's Ph.D thesis dealing with the diversity and role of ECM fungi in *Q. ilex* forests in relation to plant succession. We thank the Société Mycologique d'Ajaccio and especially A. Tristani for help with the preliminary identifications of fungal collections, the Parc Naturel Régional de Corse (P.N.R.C), the Office National des Forêts in Corte, and P. Pozzo di Borgo, M. Figarella, J. Alessandri, and P. Lepaulmier for providing facilities and encouragement. We are also grateful to C. Panaïotis who helped us to initiate this *Q. ilex* thesis project, to G. Eyssartier for identification of numerous *Cortinarius* species, to L. Riche for data entry and GIS analyses, to J. Chave for critical advice on statistical analyses of community diversity and spatial patterns, and to A. Lecerf for many helpful suggestions with the ADE-4 software. A. Ramelot, J. Jacquot, and H. Gryta helped us to collect fungi. Funding was provided by the Office National des Forêts (O.N.F.), the

Ministère de l'Ecologie (D.I.R.EN. Corse), and the Collectivité Territoriale de Corse (C.T.C.) to F. Richard. We finally thank two anonymous reviewers and S. Berch for their constructive comments that greatly improved this manuscript.

References

AFES. 1995. Référentiel pédologique. Collections Techniques et pratiques, INRA Editions, Paris.

Baar, J., Horton, T.R., Kretzer, A.M., and Bruns, T.D. 1999. Mycorrhizal colonization of *Pinus muricata* from resistant propagules after a stand-replacing wildfire. New Phytol. **143**: 409–418.

Berglund, H., and Jonsson, B.G. 2001. Predictability of plant and fungal species richness of old-growth boreal forest islands. J. Veg. Sci. **12**: 857–866.

Besag, J.E., and Diggle, P.J. 1977. Simple Monte Carlo tests for spatial patterns. Appl. Stat. **26**: 327–333.

Bills, G.F., Holtzman, G.I., and Miller, O.K., Jr. 1986. Comparison of ectomycorrhizal-basidiomycete communities in red spruce versus northern hardwood forests of West Virginia. Can. J. Bot. **64**: 760–768.

Bon, M. 1988. Champignons de France et d'Europe occidentale. Arthaud, Paris.

Brunner, I., Brunner, F., and Laursen, G.A. 1992. Characterization and comparison of macrofungal communities in an *Alnus tenuifolia* and an *Alnus crispa* forest in Alaska. Can. J. Bot. **70**: 1247–1258.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., and White, P.S. 1990. Light regimes beneath closed forest canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. **20**: 620–631.

Casgrain, P., and Legendre, P. 2001. The R package for multivariate and spatial analysis. Version 4.0 d5. User's manual. Département des sciences biologiques, Université de Montréal, Montréal.

Chazdon, R.L., and Fetcher, N. 1984. Photosynthetic light environments in a lowland tropical rainforest in Costa Rica. J. Ecol. **72**: 553–564.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science (Washington, DC), **199**: 1302–1310.

Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K., and Arianoutsou, M. 1996. Plant diversity in mediterranean-climate regions. Tree, **11**: 362–366.

Crawley, M.J. 1997. Plant ecology. 2nd ed. Blackwell Science Inc., Malden, Massachusetts.

Czárán, T.L., Hoekstra, R.F., and Pagie, L. 2002. Chemical warfare between microbes promotes biodiversity. Proc. Natl. Acad. Sci. U.S.A. **99**: 786–790.

Dahlberg, A., Jonsson, L., and Nylund, J.E. 1997. Species diversity and distribution of biomass above and below ground among ectomycorrhizal fungi in an old-growth Norway spruce forest in south Sweden. Can. J. Bot. **75**: 1323–1335.

Dahlberg, A., Schimmel, J., Taylor, A.F.S., and Johannesson, H. 2001. Post-fire legacy of ectomycorrhizal fungal communities in the Swedish boreal forest in relation to fire severity and logging intensity. Biol. Conserv. **100**: 151–161.

Deacon, J.W., and Fleming, L.V. 1992. Interactions of ectomycorrhizal fungi. *In* Mycorrhizal functioning, an integrative plant-fungal process. *Edited by* M.F. Allen. Routledge, Chapman and Hall, New York. pp. 249–300.

Esqueda-Valle, M., Perez-Silva, E., Herrera, T., Coronado-Andrade, M., and Estrada-Torres, A. 2000. Gasteromycete composition in a vegetation gradient in Sonora, Mexico. An. Inst. Biol. Univ. Nac. Auton. Mex. **71**: 39–62.

Fisher, R.A., Corbet, A.S., and Williams, C.B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. J. Anim. Ecol. **12**: 42–58.

Fogel, R. 1976. Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas-fir stand. Can. J. Bot. **54**: 1152–1162.

Gamisans, J. 1999. La végétation de la Corse. 2nd ed. Edisud, Aixen-Provence, France.

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

Goodman, D.M., and Trofymov, J.A. 1998. Comparison of communities of ectomycorrhizal fungi in old-growth and mature stands of Douglas-fir at two sites on southern Vancouver Island. Can. J. For. Res. **28**: 574–581.

Harvey, A.E., Jurgensen, M.F., and Larsen, M.J. 1978. Seasonal distribution of ectomycorrhizae in a mature Douglas-fir/Larch forest soil in Western Montana. For. Sci. **24**: 203–208.

Hawksworth, D.L. 2001. The magnitude of fungal diversity: the 1.5 million species estimate revisited. Mycol. Res. **105**: 1422–1432.

Hill, M.O., and Smith, A.J.E. 1976. Principal component analysis of taxonomic data with multi-state discrete characters. Taxon, **25**: 249–255.

Horton, T.R., and Bruns, T.D. 2001. The molecular revolution in ectomycorrhizal ecology: peeking into the black-box. Mol. Ecol. **10**: 1855–1871.

Huisman, J., and Weissing, F.J. 1999. Biodiversity of plankton by species oscillations and chaos. Nature (London), **402**: 407–410.

Jansen, A.E., and De Nie, H.W. 1988. Relations between mycorrhizas and fruitbodies of mycorrhizal fungi in Douglas fir plantations in the Netherlands. Acta Bot. Neerl. **37**: 243–249.

Jones, M.D., Durall, D.M., and Cairney, W.G. 2003. Ectomycorrhizal fungal communities in young forest stands regenerating after clearcut logging. New Phytol. **157**: 399–422.

Keizer, P.J., and Arnolds, E. 1994. Succession of ectomycorrhizal fungi in roadside verges planted with common oak (*Quercus robur* L.) in Drenthe, The Nederlands. Mycorrhiza, **4**: 147–159.

Kernaghan, G., Widden, P., Bergeron, Y., Légaré, S., and Paré, D. 2003. Biotic and abiotic factors affecting ectomycorrhizal diversity in boreal mixed-woods. Oikos, **102**: 497–504.

Laganà, A., Loppi, S., and De Dominicis, V. 1999. Relationship between environmental factors and the proportions of fungal trophic groups in forest ecosystems of the central Mediterranean area. For. Ecol. Manag. **124**: 145–151.

Last, F.T., Dighton, J., and Mason, P.A. 1987. Successions of sheathing mycorrhizal fungi. Trends Ecol. Evol. **2**: 157–161.

Malloch, D.W., Pirozynski, K.A., and Raven, P.H. 1980. Ecological and evolutionary significance of mycorrhizal symbioses in vascular plants (a review). Proc. Natl. Acad. Sci. U.S.A. **77**: 2113–2118.

Manly, B.F.J. 1997. Randomization, bootstrap and Monte Carlo methods in biology. 2nd ed. Chapman and Hall, London.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. **27**: 209–220.

Mc Carthy, J. 2001. Gap dynamics of forest trees: A review with particular attention to boreal forests. Environ. Rev. **9**: 1–59.

Médail, F., and Verlaque, R. 1997. Ecological characteristics and rarity of endemic plants from southeast France and Corsica: implications for biodiversity conservation. Biol. Conserv. **80**: 269–281.

Mehus, H. 1986. Fruit body production of macrofungi in some north Norwegian forest types. Nord. J. Bot. **6**: 679–702.

Molina, R., Massicotte, H.B., and Trappe, J.M. 1992. Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. *In* Mycorrhizal functioning, an integrative plant-fungal process. *Edited by* M.F. Allen. Routledge, Chapman and Hall, New York. pp. 357–423.

Nantel, P., and Neumann, P. 1992. Ecology of ectomycorrhizal-basidiomycete communities on a local vegetation gradient. Ecology, **73**: 99–117.

Nara, K., Nakaya, H., Wu, B., Zhou, Z., and Hogetsu, T. 2003. Underground primary succession of ectomycorrhizal fungi in a volcanic desert on Mount Fuji. New Phytol. **159**: 743–756.

Norstedt, G., Bader, P., and Ericson, L. 2001. Polypores as indicators of conservation value in Corsican pine forests. Biol. Conserv. **99**: 347–354.

O'Dell, T.E., Ammirati, J.F., and Schreiner, E.G. 1999. Species richness and abundance of ectomycorrhizal basidiomycete sporocarps on a moisture gradient in the *Tsuga heterophylla* zone. Can. J. Bot. **77**: 1699–1711.

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

Oldeman, R.A.A. 1990. Forests: elements of sylvology. Springer-Verlag, Berlin.

Panaïotis, C., Loisel, R., and Paradis, G. 1995. Dating natural gaps in the holm oak forest (*Quercus ilex* L.) in Fango MAB reserve (Corsica) by reading rings of maquis components. Ann. Sci. For. **52**: 477–487.

Panaïotis, C., Carcaillet, C., and M'hamedi, M. 1997. Determination of the natural mortality age of an holm oak (*Quercus ilex* L.) stand in Corsica (Mediterranean Island). Acta Oecol. **18**: 519–530.

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

Quézel, P., and Médail, F. 2003. Écologie et biogéographie des forêts du bassin méditerranéen. Elsevier, Paris.

Ripley, B.D. 1977. Modelling spatial patterns. J. Roy. Stat. Soc. **B39**: 172–212.

Såstad, S.M. 1995. Fungi-vegetation relationships in a *Pinus sylvestris* forest in central Norway. Can. J. Bot. **73**: 807–816.

Schmit, J.P., Murphy, J.F., and Mueller, G.M. 1999. Macrofungal diversity of a temperate oak forest: a test of species richness estimators. Can J. Bot. **77**: 1014–1027.

Signorello, P. 1996. Indagini micocenologiche sulle cenosi a *Quercus ilex* L. dell'Etna. Micol. Ital. **1**: 74–80.

Skirgiello, A. 1998. Macromycetes of oak-hornbeam forests in the Białowieża National Park– monitoring studies. Acta Mycol. **33**: 171–189.

Smith, S.E., and Read, D.J. 1997. Mycorrhizal symbiosis. 2nd ed. Academic Press, London.

Smith, J.E., Molina, R., Huso, M.M.P., Luoma, D.L., Mc Kay, D., Castellano, M.A., Lebel, T., and Valachovic, Y. 2002. Species richness, abundance, and composition of hypogeous and epigeous ECM fungal sporocarps in young, rotation-age, and old-growth stands of Douglas-fir (*Pseudotsuga menziesii*) in the Cascade Range of Oregon, U.S.A. Can. J. Bot. **80**: 186–204.

Tedersoo, L., Koljalg, U., Hallenberg, N., and Larsson, K.-H. 2003. Fine scale distribution of ectomycorrhizal fungi and roots across substrate layers including coarse woody debris in a mixed forest. New Phytol. **159**: 153–165.

Thioulouse, J., Chessel, D., Dodélec, S., and Olivier, J.M. 1997. ADE-4: a multivariate analysis and graphical display software. Stat. Comp. **7**: 75–83.

Tilman, D. 1992. Resource competition and the community structure. Princeton University Press, Princeton, New Jersey.

Villeneuve, N., Grandtner, M.M., and Fortin, J.A. 1989. Frequency and diversity of ectomycorrhizal and saprophytic macrofungi in the Laurentide Mountains of Quebec. Can. J. Bot. **67**: 2616–2629.

Vogt, K.A., Bloomfield, J., Ammirati, J.F., and Ammirati, S.R. 1992. Sporocarp production by basidiomycetes, with emphasis on forest ecosystems. *In* The fungal community: its organization and role in the ecosystem. *Edited by* G.C. Carroll and D.T. Wicklow. Marcel Dekker, Inc., New York. pp 563–581.

Ward, J.H. 1963. Hierarchical grouping to optimise on objective function. J. Am. Stat. Assoc. **58**: 236–244.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon, **21**: 213–251.

Yamada, A., and Katsuya, K. 2001. The disparity between the number of ectomycorrhizal fungi and those producing fruit bodies in a *Pinus densifolia* stand. Mycol. Res. **105**: 957–965.

Appendix A

Appendix appears on the following page.

Table A1. List of ECM species and information related to their fruiting pattern during the period 1999–2002.

Species	FR*	$A^{\dagger}$	SF‡	$D^{\S}$	$P^{\|\|}$	$C^{\P}$	Host range	Group#
Amanita caesarea (Scop.: Fr.) Pers.	3	37	28.1 (18)	19	9	100–200	Thermophilic	F
Amanita citrina (Schaeff.) Pers.	3	29	28.1 (18)	43	25	60–100	Broad host range	C
Amanita franchetii (Boud.) Fayod	1	1^{R}	1.6 (1)	1	35	60–100	Broad host range	D
Amanita gioiosa Curreli ex Curreli	1	1^{R}	1.6 (1)	1	7	60–100	Chaparral restricted	E
Amanita junquillea Quél.	2	34	31.2 (20)	7	14	50–100	Thermophilic	E
Amanita malleata (Piane ex Bon) Contu	1	5^{R}	7.8 (5)	10	14	60–120	Broad host range	D
Amanita pantherina (D.C.: Fr.) Krombh.	3	26	29.7 (19)	25	21	60–100	Broad host range	C
Amanita phalloides (Fr.: Fr.) Link.	2	10	7.8 (5)	43	14	60–120	Broad host range	D
Amanita rubescens (Pers.: Fr.) S. F. Gray	1	1^{R}	1.6 (1)	1	21	100–180	Broad host range	F
Amanita spissa (Fr.) Kumm.	1	3^{R}	3.1 (2)	3	7	100–180	Angiosperms linked	D
Amanita vaginata (Bull.: Fr.) Vitt.	2	5^{R}	7.8 (5)	41	21	60–120	Broad host range	D
Aureoboletus gentilis (Quél.) Pouz.	3	20	23.4 (15)	26	14	30–70	Broad host range	C
Boletus aereus Bull.: Fr.	1	1^{R}	1.6 (1)	1	21	150–300	Thermophilic	F
Boletus edulis Bull.: Fr.	1	1^{R}	1.6 (1)	1	7	120–250	Broad host range	F
Boletus erythropus Pers.: Fr.	1	1^{R}	1.6 (1)	1	14	150–200	Broad host range	F
Boletus queletii Schulz.	2	2^{R}	3.1 (2)	1	21	150–200	Angiosperms linked	F
Boletus rhodoxanthus (Krombh.) Kallenb.	1	1^{R}	1.6 (1)	1	42	120–200	Thermophilic	F
Boletus satanas Lenz	1	1^{R}	1.6 (1)	1	14	200–300	Thermophilic	F
Cantharellus cibarius (Fr.: Fr.) Fr.	2	54	35.9 (23)	40	42	50–120	Broad host range	C
Cortinarius balaustinus J. E. Lange	1	3^{R}	3.1 (2)	1	7	40–80	Angiosperms linked	D
Cortinarius subgen. *Phlegmacium* sect. *Bulbopodium*-1	1	1^{R}	1.6 (1)	—	—	—	—	—
Cortinarius subgen. *Phlegmacium* sect. *Bulbopodium*-2	1	1^{R}	1.6 (1)	—	—	—	—	—
Cortinarius subgen. *Phlegmacium* sect. *Bulbopodium*-3	1	1^{R}	1.6 (1)	—	—	—	—	—
Cortinarius subgen. *Phlegmacium* sect. *Bulbopodium*-4	1	1^{R}	1.6 (1)	—	—	—	—	—
Cortinarius subgen. *Phlegmacium* sect. *Bulbopodium* 5	1	1^{R}	1.6 (1)	—	—	—	—	—
Cortinarius caerulescens (Schaeff.) Fr.	2	7	7.8 (5)	16	21	80–120	Broad host range	D
Cortinarius caligatus Malençon	1	3^{R}	3.1 (2)	8	35	30–60	Thermophilic	F
Cortinarius (group) *calochrous* (Pers.:Fr.) Fr.	3	14	17.2 (11)	13	35	50–70	Broad host range	C
Cortinarius dionysae Rob. Henry	1	1^{R}	1.6 (1)	1	21	50–80	Broad host range	D
Cortinarius duracinus Fr.	1	13	14.1 (9)	37	21	50–100	Broad host range	D
Cortinarius elatior Fr.	3	66	51.6 (33)	55	35	100–150	*Quercus* linked	B
Cortinarius georgiolens Rob. Henry	1	1^{R}	1.6 (1)	1	35	60–140	*Quercus ilex* specific	F
Cortinarius infractus (Pers.: Fr) Fr.	3	17	15.6 (10)	11	12	50–120	Broad host range	C
Cortinarius largodelibutus Rob. Henry	1	6^{R}	6.2 (4)	8	35	60–120	*Quercus ilex* specific	F
Cortinarius luteocingulatus Cheype	2	6^{R}	6.2 (4)	9	46	50–100	*Quercus ilex* specific	F
Cortinarius misermontii Chevassut & Rob. Henry	1	1^{R}	1.6 (1)	1	35	60–90	*Quercus ilex* specific	F
Cortinarius subgen. *Myxacium*-1	2	3^{R}	4.7 (3)	—	—	—	—	—
Cortinarius subgen. *Myxacium*-2	1	1^{R}	1.6 (1)	—	—	—	—	—
Cortinarius subgen. *Myxacium*-3	1	1^{R}	1.6 (1)	—	—	—	—	—
Cortinarius subgen. *Myxacium*-4	1	6^{R}	1.6 (1)	1	21	—	—	—
Cortinarius ochraceocephalus Bidaud et al.	1	8	6.2 (4)	21	35	80–120	*Quercus ilex* specific	F
Cortinarius subgen. *Phlegmacium*-1	1	1^{R}	1.6 (1)	—	—	—	—	—
Cortinarius subgen. *Phlegmacium*-2	1	1^{R}	1.6 (1)	—	—	—	—	—
Cortinarius subgen. *Phlegmacium*-3	1	1^{R}	1.6 (1)	—	—	—	—	—
Cortinarius subgen. *Phlegmacium*-4	1	2^{R}	1.6 (1)	—	—	—	—	—
Cortinarius subgen. *Phlegmacium*-5	1	4^{R}	1.6 (1)	—	—	—	—	—
Cortinarius (group) *privignus* (Fr.) Fr.	1	3^{R}	4.7 (3)	1	7	50–80	Broad host range	D
Cortinarius pseudosalor J.E. Lange	2	4^{R}	4.7 (3)	25	21	60–100	Angiosperms linked	D
Cortinarius purpurascens (Fr.) Fr.	2	3^{R}	4.7 (3)	7	14	100–150	Broad host range	D
Cortinarius purpurascens f. *elatus* Rob. Henry.	1	1^{R}	1.6 (1)	1	35	20–50	Thermophilic	F
Cortinarius salor Fr.	1	3^{R}	4.7 (3)	1	7	50–100	Broad host range	D

Table A1 (*continued*).

Species	FR*	$A^{\dagger}$	SF‡	$D^{\S}$	$P^{\|\|}$	$C^{\P}$	Host range	Group#
Cortinarius subgen. *Sericeocybe*-1	2	4^{R}	6.2 (4)	—	—	—	—	—
Cortinarius subturibulosus Kizlik & Trescol	1	1^{R}	1.6 (1)	1	21	30–60	*Quercus ilex* specific	F
Cortinarius subgen. *Telamonia*-1	1	1^{R}	1.6 (1)	—	—	—	—	—
Cortinarius subgen. *Telamonia*-2	3	8	6.2 (4)	—	—	—	—	—
Cortinarius trivialis J.E. Lange	2	8	6.2 (4)	1	14	50–100	Angiosperms linked	D
Cortinarius (group) *varius* (Schaeff.: Fr.) Fr.	1	1^{R}	1.6 (1)	1	21	80–120	Angiosperms linked	D
Craterellus cornocopioides (L.: Fr.) Pers.	3	46	6.2 (4)	24	42	50–150	Angiosperms linked	C
Hebeloma crustuliniforme (Bull.) Quél.				13	35		Broad host range	D
Hebeloma sp.	1	4^{R}	3.1 (2)	—	—	—	—	—
Hebeloma mesophaeum (Pers.) Quél.	2	5^{R}	4.7 (3)	10	28	50–80	Broad host range	D
Hebeloma sinapizans (Paul.) Gillet	3	15	9.4 (6)	15	18	80–150	Broad host range	C
Hebeloma versipelle (Fr.) Gillet	1	3^{R}	1.6 (1)	1	7	50–80	Broad host range	D
Helvella sulcata Afz.: Fr.	1	1^{R}	1.6 (1)	1	42	30–50	Broad host range	F
Humaria hemisphaerica (Wigg.: Fr.) Fuck.	1	1^{R}	1.6 (1)	1	42	20–30	Angiosperms linked	F
Hydnellum concrescens (Pers.) Banker	2	12	14.1 (9)	65	18	20–70	Broad host range	C
Hydnellum ferrugineum (Fr.: Fr.) P. Karst.	1	4^{R}	3.1 (2)	1	21	30–90	Broad host range	D
Hydnum repandum L.: Fr.	3	139	31.2 (20)	36	42	80–150	Broad host range	B
Hydnum rufescens Schum.: Fr.	1	10	3.1 (2)	9	28	40–70	Broad host range	D
Hygrophorus cossus (Sow.) Fr.	2	49	39.1 (25)	43	46	50–70	*Quercus* linked	C
Hygrophorus eburneus var. *carneipes* Kühner	1	6^{R}	4.7 (3)	1	140	50–70	*Quercus* linked	E
Hygrophorus nemoreus (Pers.: Fr.) Fr.	2	55	35.9 (23)	43	21	80–120	*Quercus* linked	C
Hygrophorus persoonii Arnolds	3	23	21.9(14)	40	28	50–80	*Quercus* linked	C
Hygrophorus russula (Schaeff.: Fr.) Quél.	3	117	46.9 (30)	26	26	120–200	*Quercus* linked	B
Inocybe cervicolor (Pers.) Quél.	2	12	7.8 (5)	75	32	40–60	Broad host range	C
Inocybe flocculosa (Berk.) Sacc.	2	46	28.1 (18)	12	25	30–50	Broad host range	F
Inocybe geophylla (Bull.: Fr.) Kumm.	1	58	32.8 (21)	30	42	30–50	Broad host range	F
Inocybe geophylla var. *lilacina* (Peck) Gillet	1	14	9.4 (6)	9	56	30–50	Broad host range	F
Inocybe subgen. *Inocybe*-1	1	5^{R}	1.6 (1)	—	—	—	—	—
Inocybe subgen. *Inocybium*-1	1	1^{R}	1.6 (1)	—	—	—	—	—
Inocybe subgen. *Inocybium*-2	1	1^{R}	1.6 (1)	—	—	—	—	—
Inocybe subgen. *Inocybium*-3	1	3^{R}	3.1 (2)	—	—	—	—	—
Inocybe subgen. *Inocybium*-4	1	2^{R}	1.6 (1)	—	—	—	—	—
Inocybe subgen. *Inosperma*-1	1	1^{R}	1.6 (1)	—	—	—	—	—
Inocybe obscura (Pers.) Gillet	1	36	17.2 (11)	18	56	30–50	Broad host range	F
Inocybe pudica Kühner (*I. whitei* ss. Kuyper)	1	1^{R}	1.6 (1)	1	56	40–60	Broad host range	D
Inocybe tigrina R. Heim	1	352	84.4 (54)	72	42	30–50	Angiosperms linked	A
Laccaria laccata (Scop.: Fr.) Berk. & Broome	3	421	64.1 (41)	38	35	10–30	Broad host range	A
Lactarius acerrimus Britzelm.	1	1^{R}	1.6 (1)	1	21	100–150	*Quercus* linked	D
Lactarius camphoratus (Bull.) Fr.	1	1^{R}	1.6 (1)	1	7	50–70	*Quercus* linked	D
Lactarius chrysorrheus Fr.	3	376	65.6 (42)	39	23	50–100	*Quercus* linked	A
Lactarius fuliginosus (Fr.: Fr.) Fr.	2	4^{R}	6.2 (4)	8	14	60–80	*Quercus* linked	C
Lactarius rufus (Scop.: Fr.) Fr	2	7	7.8 (5)	44	60	50–100	Broad host range	C
Lactarius cistophilus Bon & Trimbach.	1	2^{R}	1.6 (1)	1	7	30–80	Chaparral restricted	E
Lactarius rubrocinctus Fr.	3	47	28.1 (18)	50	14	30–60	Angiosperms linked	C
Lactarius uvidus (Fr.: Fr.) Fr.	2	17	17.2 (11)	18	42	50–80	Broad host range	D
Lactarius zonarius (Bull.) Fr.	3	4^{R}	4.7 (3)	14	19	80–120	*Quercus* linked	C
Leccinum corsicum (Rolland) Singer	1	4^{R}	6.2 (4)	30	56	100–150	Chaparral restricted	E
Leccinum lepidum (Bouchet ex Essette) Quadr.	3	16	20.3 (13)	32	42	100–150	*Quercus ilex* specific	C
Leccinum sp.	1	1^{R}	1.6 (1)	—	—	—	—	—
Peziza badia Pers.: Fr.	2	16	4.7 (3)	13	35	50–100	Broad host range	D
Phellodon melaleucus (Swartz: Fr.) P. Karst.	1	3^{R}	4.7 (3)	21	35	50–100	Angiosperms linked	D
Phellodon tomentosus (L.: Fr.) Banker	1	3^{R}	3.1 (2)	6	21	40–80	Broad host range	D
Ramaria aurea (Schaeff.) Quél.	1	1^{R}	1.6 (1)	1	28	80–150	Broad host range	D
Ramaria botrytis (Pers.: Fr.) Ricken	1	4^{R}	3.1 (2)	1	28	80–150	Angiosperms linked	D
Ramaria formosa (Pers.: Fr.) Quél.	1	1^{R}	1.6 (1)	1	7	80–150	Angiosperms linked	D
Russula acrifolia Romagn.	3	137	68.7 (44)	27	14	80–150	Broad host range	B

Table A1 (*continued*).

Species	FR*	$A^{\dagger}$	SF[‡]	$D^{\S}$	$P^{\|\|}$	$C^{\P}$	Host range	Group[#]
Russula amoenicolor f. *nigrosanguinea* Romagn.	1	15	6.2 (4)	13	7	50–80	Angiosperms linked	D
Russula atropurpurea Krombh. (non Peck)	1	4^{R}	4.7 (3)	7	14	80–150	Broad host range	D
Russula aurea f. *axantha* Romagn.	1	1^{R}	1.6 (1)	1	35	60–100	Thermophilic	F
Russula chloroides (Krombh.) Bres.	3	64	39.1 (25)	19	18	60–120	Broad host range	C
Russula cistoadelpha M. Moser & Trimbach	1	4^{R}	4.7 (3)	1	7	40–60	Chaparral restricted	E
Russula sp. sect. *Compactae*	1	2^{R}	1.6 (1)	—	—	—	—	—
Russula decipiens (Singer) Svrèek	2	28	28.1 (18)	50	35	100–150	*Quercus* linked	C
Russula sect. *Decolorantes*-1	1	1^{R}	1.6 (1)	—	—	—	—	—
Russula sect. *Decolorantes*-2	1	3^{R}	4.7 (3)	—	—	—	—	—
Russula delica Fr.	2	74	53.1 (34)	19	21	120–200	*Quercus* linked	B
Russula densifolia Secr. ex Gillet	1	4^{R}	4.7 (3)	21	21	50–80	Angiosperms linked	D
Russula faustiana Sarnari	2	14	12.5 (8)	15	14	50–70	*Quercus ilex* specific	F
Russula foetens Pers.: Fr.	2	9	10.9 (7)	21	21	100–200	Broad host range	F
Russula fragilis (Pers.: Fr.) Fr.	2	80	57.8 (37)	54	21	20–60	*Quercus* linked	B
Russula pseudoaeruginea f. *galochroa* Sarnari	1	3^{R}	1.6 (1)	1	35	30–40	Thermophilic	F
Russula gilvescens Romagn. ex Bon	1	6^{R}	7.8 (5)	21	35	50–100	Thermophilic	F
Russula globispora J. Blum ex Bon	1	45	35.9 (23)	41	14	80–120	*Quercus ilex* specific	C
Russula grisea Fr.	3	14	14.1 (9)	8	16	80–120	Angiosperms linked	C
Russula heterophylla (Fr.) Fr.	1	12	7.8 (5)	7	21	80–150	*Quercus* linked	C
Russula sect. *Ingratae*-1	2	5^{R}	4.7 (3)	—	—	—	—	—
Russula laricino-affinis Bon	1	42	39.1 (25)	28	21	30–60	*Quercus ilex* specific	C
Russula laurocerasi Melzer	1	1^{R}	1.6 (1)	1	35	80–120	Broad host range	D
Russula sect. *Lilaceae*	1	2^{R}	3.1 (2)	—	—	—	—	—
Russula nitida (Pers.: Fr.) Fr.	2	2^{R}	3.1 (2)	1	21	60–80	Angiosperms linked	D
Russula nuragica Sarnari	1	7	4.7 (3)	1	14	60–150	*Quercus ilex* specific	F
Russula ochroleuca Pers.	1	5^{R}	6.2 (4)	25	21	80–120	Broad host range	D
Russula ochrospora (Nicolaj ex Quadr. & W. Rossi) Quadr.	1	28	25 (16)	44	21	60–100	Thermophilic	F
Russula olivacea (Schaeff.) Pers.	3	78	64.1 (41)	62	14	100–150	Broad host range	B
Russula pectinatoides Peck (ss. Romagn.)	1	1^{R}	1.6 (1)	1	14	40–80	Broad host range	D
Russula persicina var. *rubrata* Romagn.	3	33	32.8 (21)	26	21	40–80	*Quercus* linked	C
Russula poikilochroa Sarnari	1	13	6.2 (4)	19	14	30–60	Thermophilic	F
Russula poikilochroa f. *heliochroma* Sarnari	1	2^{R}	1.6 (1)	1	7	30–60	Thermophilic	F
Russula sect. *Polychromae*	2	13	15.6 (10)	—	—	—	—	—
Russula rhodomarginata Sarnari	1	2^{R}	1.6 (1)	1	35	30–50	Thermophilic	E
Russula rhodomelaena Sarnari	1	1^{R}	1.6 (1)	1	42	40–60	*Quercus* linked	F
Russula risigallina f. *chamaeleontina* (Batsch) Sacc.	1	106	53.1 (34)	19	14	30–70	*Quercus* linked	C
Russula seperina Dupain	1	14	6.2 (4)	1	14	30–60	*Quercus* linked	D
Russula sect. *Tenellae*-1	2	19	20.3 (13)	—	—	—	—	—
Russula sect. *Tenellae*-2	1	1^{R}	1.6 (1)	—	—	—	—	—
Russula tyrrhenica Sarnari	1	1^{R}	1.6 (1)	1	35	100–200	Chaparral restricted	E
Russula vesca Fr.	3	19	25 (16)	8	35	50–90	Broad host range	C
Russula vinosobrunnea var. *paraolivacea* Bon	1	2^{R}	3.1 (2)	1	14	80–120	Thermophilic	F
Russula xerampelina (Schaeff.) Fr.	1	5^{R}	7.8 (5)	5	7	80–120	Broad host range	D
Sarcodon cyrneus Maas G.	2	12	4.7 (3)	5	21	100–150	Thermophilic	F
Scleroderma verrucosum (Bull.: Pers.) Pers.	2	28	9.4 (6)	7	21	30–50	Angiosperms linked	F
Thelephora palmata (Scop.: Fr.) Fr.	1	1^{R}	1.6 (1)	1	21	20–50	Broad host range	F
Thelephora sp. 1	1	1^{R}	1.6 (1)	—	—	—	—	—
Thelephora sp. 2	1	1^{R}	1.6 (1)	—	—	—	—	—
Tricholoma atrosquamosum (Chev.) Sacc.	3	36	34.4 (22)	28	32	70–100	Broad host range	C
Tricholoma portentosum (Fr.: Fr.) Quél.	1	6^{R}	3.1 (2)	1	56	100–150	Broad host range	D
Tricholoma pseudoalbum Bon	1	2^{R}	1.6 (1)	1	14	80–140	Angiosperms linked	D
Tricholoma saponaceum (Fr.: Fr.) Kumm.	3	76	46.9 (30)	68	44	100–150	Broad host range	B
Tricholoma sp.	1	1^{R}	1.6 (1)	—	—	—	—	—
Tricholoma sect. *Atrosquamosa*	1	3^{R}	3.1 (2)	—	—	—	—	—

Table A1 (*concluded*).

Species	FR*	$A^{\dagger}$	SF‡	$D^{\S}$	$P^{\|\|}$	$C^{\P}$	Host range	Group#
Tricholoma stans (Fr.) Sacc.	1	1^R	1.6 (1)	1	7	60–90	Thermophilic	F
Tricholoma ustale (Fr.: Fr.) Kumm.	2	6^R	7.8 (5)	48	35	60–90	Angiosperms linked	D
Xerocomus armeniacus (Quél.) Quél.	1	1^R	1.6 (1)	1	7	50–90	Broad host range	D
Xerocomus spadiceus (Fr.) Quél.	1	6^R	7.8 (5)	44	49	60–100	Broad host range	D

Note: For each determined species, seven life history traits are documented (temporal variation in fruitbody production, abundance, spatial frequency, duration of fruiting period, periodicity, breadth of host range, and mean diameter of the fruitbody cap), as well as group according to the Hill and Smith (1976) analysis.

*Fruiting regularity determined as the number of seasons of occurrence.

†Abundance determined as the number of fruitbodies over 3 years. Rare taxa (i.e., taxa that produced less than 1 fruitbody per 1000 m^2 on average) are indicated with a superscripted R.

‡Spatial frequency determined as the percentage of the total number of plots occupied, with the number of plots given in parenthesis.

§Duration (number of days) of fruiting period.

||Periodicity determined as the number of days between the production peak and the beginning of the fruiting season.

¶Mean diameter (mm) of the fruitbody cap.

#Groups according to the Hill and Smith (1976) analysis.

Table A2. List of saprobic species and information related to their fruiting pattern (temporal variation in fruitbody production, abundance, and spatial frequency) over the 3-year survey.

Species	FR†	$A^{\ddagger}$	SF§
Agaricus depauperatus (Møller) Pilàt	2	4^R	6.2 (4)
Agaricus haemorrhoidarius Schulz.	2	8	12.5 (8)
Agaricus porphyrizon P.D. Orton	1	1^R	1.6 (1)
Agaricus sp. sect. *Agaricus*	3	9	10.9 (7)
Agaricus silvaticus Schaeff.: Fr.	2	6^R	9.4 (6)
Aleuria aurantia (Pers.: Fr.) Fuckel	1	1^R	1.6 (1)
Armillaria mellea (Vahl: Fr.) Kumm.	2	26	4.7 (3)
Calocybe carnea (Bull.: Fr.) Donk	2	15	10.9 (7)
Clavulina cinerea (Bull.: Fr.) Schröt.*	3	110	48.4 (31)
Clavulina cristata (Holmsk.: Fr.) Schröt.*	1	21	10.9 (7)
Clavilunopsis corniculata (Schaeff.: Fr.) Corner*	1	2^R	1.6 (1)
Clavilunopsis helvola (Pers.: Fr.) Corner*	1	6^R	4.7 (3)
Clitocybe costata Kühner & Romagn.	2	7	6.2 (4)
Clitocybe gibba (Pers.: Fr.) Kumm.	3	77	26.6 (17)
Clitocybe odora (Bull.: Fr.) Kumm.	1	22	1.6 (1)
Clitocybe radicellata Gillet	1	3^R	4.7 (3)
Clitocybe sp. sect. *Infundibuliformes*	1	1^R	1.6 (1)
Clitopilus prunulus (Scop.: Fr.) Kumm.*	2	23	18.8 (12)
Collybia butyracea (Bull.: Fr.) Kumm.*	2	92	26.6 (17)
Collybia dryophila (Bull.: Fr.) Kumm.*	2	77	21.9 (14)
Collybia kuehneriana Singer*	2	19	6.2 (4)
Coltricia perennis (L.: Fr.) Murrill	1	2^R	3.1 (2)
Conocybe tenera (Schaeff.: Fr.) Fayod	1	5^R	1.6 (1)
Coprinus atramentarius (Bull.: Fr.) Fr.	1	9	3.1 (2)
Coprinus cinereus (Schaeff.: Fr.) S.F. Gray	1	1^R	1.6 (1)
Coprinus micaceus (Bull.: Fr.) Fr.	1	1^R	1.6 (1)
Coprinus picaceus (Bull.: Fr.) Fr.	1	1^R	1.6 (1)
Coprinus sp. sect. *Coprinus*	1	1^R	1.6 (1)
Cuphophyllus pratensis (Pers.: Fr.) Bon*	1	1^R	1.6 (1)
Entoloma corvinum (Kühner) Noordel.*	2	38	10.9 (7)
Entoloma lividoalbum (Kühner & Romagn.) Kubicka*	1	1^R	1.6 (1)
Entoloma nidorosum (Fr.) Quél.*	3	159	45.3 (29)
Geoglossum cookeianum Nannf.*	1	2^R	1.6 (1)
Hygrocybe conica (Scop.: Fr.) Kumm.	3	10	12.5 (8)
Hygrocybe sp. sect. *Macrosporae*	1	1^R	1.6 (1)
Hygrocybe tristis (Pers.) Møller	1	1^R	1.6 (1)
Lepiota castanea Quél.	1	1^R	1.6 (1)
Lepiota sp.	1	2^R	1.6 (1)

Table A2 (*concluded*).

Species	FR[†]	*A*[‡]	SF[§]
Lepiota subincarnata J. E. Lange	1	3[R]	1.6 (1)
Lepista nuda (Bull.: Fr.) Cooke	2	3[R]	3.1 (2)
Leucopaxillus gentianeus (Quél.) Kotlaba*	3	42	7.8 (5)
Leucopaxillus sp.*	1	2[R]	3.1 (2)
Leucopaxillus tricolor (Peck) Kühner*	1	5[R]	3.1 (2)
Lycoperdon sp.	1	1[R]	1.6 (1)
Lycoperdon perlatum Pers.: Pers.	3	225	26.6 (17)
Lycoperdon pyriforme Schaeff.: Pers.	2	5[R]	4.7 (3)
Lyophyllum immundum (Berk.) Kühner	2	9	10.9 (7)
Lyophyllum leucophaeatum (P. Karst.) P. Karst.	1	2[R]	3.1 (2)
Macrolepiota procera (Scop.: Fr.) Singer	3	9	6.2 (4)
Macrolepiota nympharum (Kalchbr.) Wasser	1	4[R]	3.1 (2)
Marasmius collinus (Scop.:Fr.) Singer	2	5[R]	3.1 (2)
Mycena alcalina (Fr.: Fr.) Kumm.*	2	133	6.2 (4)
Mycena galericulata (Scop.: Fr.) S.F. Gray*	1	5[R]	1.6 (1)
Mycena sp. 1*	1	7	7.8 (5)
Mycena sp. 2*	1	6[R]	1.6 (1)
Mycena pura (Pers.: Fr.) Kumm.*	3	71	23.4 (15)
Mycena pura var. *rosea* (Bull.) Gillet*	1	5[R]	3.1 (2)
Mycena vulgaris (Pers.: Fr.) Kumm.*	1	10	1.6 (1)
Mycena vitilis (Fr.) Quél.*	2	290	40.6 (26)
Pluteus depauperatus Romagn.	1	6[R]	6.2 (4)
Pluteus salicinus (Pers.: Fr.) Kumm.	2	4[R]	4.7 (3)
Pluteus thomsonii (Berk. & Broome) Dennis	1	1[R]	1.6 (1)
Psathyrella candolleana (Fr.: Fr.) Maire	2	3[R]	4.7 (3)
Rhodocybe mundula (Lasch) Singer	1	1[R]	1.6 (1)
Tubaria furfuracea (Pers.: Fr.) Gillet*	1	9	9.4 (6)
Vascellum pratense (Pers.) Kreisel	1	9	1.6 (1)
Xerula radicata (Rehl.:Fr.) Dörfelt	2	5[R]	1.6 (1)
Xylaria hypoxylon (L.: Fr.) Grev.	1	5[R]	1.6 (1)

*Species for which vouchers have been deposited at the herbarium of the Evolution et Diversité Biologique Laboratory (Unité mixte de recherche 5174, Université Toulouse III Paul Sabatier, Toulouse, France). Vouchers are available upon request.

[†]Fruiting regularity determined as the number of seasons of occurrence.

[‡]Abundance determined as the number of fruitbodies over 3 years. Rare taxa (i.e., taxa that produced less than 1 fruitbody per 1000 m^2 on average) are indicated with a superscripted R.

[§]Spatial frequency determined as the percentage of the total number of plots occupied, with number of plots within parenthesis.