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Linking biodiversity to mutualistic networks – woody species and ectomycorrhizal fungi

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Abstract. Mutualistic interactions are currently mapped by bipartite networks with particular architecture and properties. The mycorrhizae connect the trees and permit them to share resources, therefore relaxing the competition. Ectomycorrhizal macrofungi associated with woody species (*Quercus robur, Q. cerris, Q. petraea, Tilia tomentosa, Carpinus betulus, Corylus avellana,* and *Q. pubescens*) growing in a temperate, broadleaved mixed forest, from a hilly area near the city of Cluj–Napoca, central Romania were included in a bipartite mutualistic network. Community structure was investigated using several network metrics, modularity and nestedness algorithms in conjunction with C-score index cluster analysis and nonmetric multidimensional scaling (the Kulczynski similarity was index used as most appropriate metric selected by minimal stress criterion). The results indicate that the network presents high asymmetry (hosts are outnumbered by mycobionts at a great extent), high connectance, low modularity, and high nestedness, competition playing a secondary role in community assemblage (non significant difference between simulated and observed C-score). The nestedness pattern is non-random and is comparable to previously published results for other similar interactions containing plants. In the proposed network, woody species function exclusively as generalists. Modularity analysis is a finer tool were identifying species roles than centrality measures, however, the two types of algorithms permit the separation of species according to their roles as for example connectors (generalist species) and ultraperipheral species (specialists). Supergeneralist woody species function as hubs for the diverse ectomycorrhizal community while supergeneralist ectomycorrhizal fungi glue the hubs into a coherent aggregate.
Keywords temperate broadleaved mixed forest, ectomycorrhizal fungi, mutualistic bipartite networks, nestedness, modularity, connectance, C-score cluster analysis, non metric multidimensional scaling.

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Introduction

Biodiversity became an iconic topic in theoretical and applied ecology during the last decades, everything being under the paradigmatic statement "nature is complex" (May & Oster 1976). The way of species co-existence within infracommunities and metacommunities is also a major issue in community ecology, alternative hypotheses being proposed and tested with time: species are randomly distributed, a phenomenon driven by stochastic processes or are non-randomly distributed as a consequence of niche partitioning, phylogenetic signal or environmental filtering (Webb 2000, Leibold 2006). Assembly rules determine the structure of natural communities (Weiher & Keddy 1999), generating hypothetical patterns of species distributions within metacommunities: nested subsets of species within regional pool, checkerboard distribution of species, Clementsian and Glesonian gradiens, evenly spaced gradient and random pattern (Leibold 2002). Among those, commonly occurring patterns of species distributions are: checkerboards of exclusive replacement meaning less species co-occurrence than expected by chance (Diamond 1975, Connor & Simberloff 1979, Gotelli & McCabe 2002) and the opposite, nested assemblages when species composing smaller sets of local communities or infracommunities are subsets of richer assemblages (Patterson & Atmar 1986).

Extracting community structure which incorporates biodiversity and assembly rules became a main trend generating a plethora of quantitative approaches. By using this interesting new and promising modeling tool, ecological networks have emerged during the last few years. Network theory brings order to an apparently orderless world, reducing complex problems to a series of relationships that can be mapped. It became obvious that information on species interactions and the quantitative approach to this ecological topic could improve the predictions on the fate biodiversity (Ingram & Steel 2010), since species interactions were playing important roles in community persistence and structure (Fortuna et al. 2010). Ecological networks incorporate trophic webs, mutualistic and parasitic interactions as well other types of biotic and abiotic interactions. The information provided by network analysis comes to widen our understanding on community pattern and species assemblage rules.

Graph theory facilitated the study of complex systems in many areas where the configuration of the interactions was important in understanding system behavior (Lurgi & Robertson 2011). Network analysis is connected to ecological complexity, a basic property of the biological world (Jordano 2010), defined in terms of the number of interacting species and the frequency of their interactions (May 1972). One of the first approaches pioneering in the area of graph theory applications to the study of biological systems was performed by May (1972), who constructed a random network of N nodes (species) and C links with an average interaction strength of σ as a model in the context of complexity-stability debate.

A network / graph is defined as a set of vertices connected by a set of links or edges. An edge is a line emanating from a vertex i to the vertex j. The mutualistic interactions are depicted by bipartite networks, with interactions occurring between two groups of species generally between two trophic levels, but not within each group (Williams 2011).

During the last decade, the area of plant-animal mutualistic interactions using network representation and analysis registered a rapid pace. Host – parasite / mutualist interactions are set in a community context and are subjected to ecological pressures in a similar way to prey-predator interaction or facilitation type interactions (Thrall et al. 2006) traditionally subjected to network analyses. Plant-pathogen and plant-mutualistic networks including fungi as partners are still emerging areas of scientific interest (Vacher et al. 2010, Fodor 2011) and less information has been accumulated on their topologies and properties.

Bipartite mutualistic networks were employed to study interactions such as those between plants and their pollinators, seed dispersers (Donatti et al. 2011), pathogens, occasionally mycorrhizal partners (Montesinos-Navarro et al. 2012), between insects and their parasitoids, plant facilitation relationships (Saavedra et al. 2008) or cleaning mutualism (Sazima et al. 2010). One of the main conclusions are that mutualistic and parasitic networks are more stable in their evolution than predator-prey networks which are more flexible (Scotti et al. 2007), these traits being evident from the network architecture analysis.

A common feature for all ecological networks is their heterogeneity in terms of the architecture of links (number of links per vertex) and non-randomness in species assemblage. However, mutualistic networks are characterized by several properties which make them different from trophic webs: strong interaction asymmetry in interaction strength, nestedness, highly skewed degree distribution with many species showing few lenfs and few species diplaying many links (Jordano et al. 2003, Bascompte et al. 2006, Vázquez et al. 2009, Thébault & Fontaine 2010), high interaction diversity, low connectance (Olesen et al. 2005, Williams 2011, Verdú & Valiente-Banuet 2008, Gonzáles et al. 2010) and modularity meaning that distinct subsets of species interact more strongly among themselves than with species from other modules (Olesen et al. 2007, Fortuna et al. 2010). The role of each species in these diverse assemblages depends on the number of interactions it establishes with potential partner species (Jordano 2010).

Trees function as ecosystem engineers since they provide multiple resources (Jones et al. 1994) and they strongly modify biotic and abiotic conditions (Olff et al. 2009). Mycorrhizae represent one of the key mutualistic relationships that shape terrestrial ecosystems. In forest ecosystems, ectomycorrhizae are dominant within mycorrhizal communities associated with woody species, and encompass an important share of biodiversity. Woody species from fam. Fagaceae, Pinaceae, Salicaceae, Betulacee, Tiliaceae in holarctic and temperate regions harbor ectomycorrhizal fungi, the majority being placed in the orders Pezizales, Helotiales, Boletales, Agaricales, Telephorales, Russulales, Phallales, Polyporales & Cantharelalles (De Roman et al. 2005, Tedersoo et al. 2010). Modern approaches to community ecology put greater emphasis on the distribution of resources and partition among plants and mycorrhizae seem to reduce the dominance of more aggressive plant competitors in plant communities (Wilkinson 1998). Depending on the circumstances, woody species may share common mycorrhizal taxa, hence, a common mycorrhizal network also in a physical sense. Therefore, a new perspective on plant communities derives from the study of the diverse mycorrhizal networks (Selosse et al. 2006), because trees have the peculiar attribute of accumulating high levels of biodiversity during their long lifetime (Petit & Hamper 2006), mycorrhizal partners included. They also share a long co-evolutionary history with their mutualists (Tedersoo et al. 2010).

It is considered true that mutualistic relationships at large have molded biodiversity (Thomson 1994, Bascompte et al. 2006) and the growing interest in their study is motivated by the increasing extinction threats affecting mutualistic species (Bascompte & Jordano 2007, Campbell et al. 2011) . The interaction between mycorrhizal partners is an indirect trophic relationship with different currencies for each member: nutrients and water versus energy (Hooper et al. 2005, Perry & Choquette 1987). Inclusion of ECM fungi in model ecosystems is of fundamental importance because they mediate most important interactions between primary producers and detrital food webs (Southworth et al. 2005). In forest ecosystems, the richness and diversity of ECM communities contrasts strongly with the low number of tree species, given the number of identified associates of the trees in the present study. The ECM fungi differ in their ability to exploit soil nutrients; this diversity may explain their distribution within different ecological niches (Bruns 1995).

In bipartite networks, diversity of species within each group may be linked to important network properties that can be translated into community level properties: for instance, network centrality measures help with the identification of the most influential species in terms of association, competition or resource use.

Nestedness is an effective tool for analyzing interaction diversity (Dyer et al. 2010), the later being defined as the number of interactions linking species in a dynamic community (Thomson 1994), an important concept going beyond the classical frame of documenting species and their diversity (Tylianakis et al. 2007). The concept was first defined in the frame of biogeography: small communities forming proper subsets of larger communities (Atmar & Patterson 1993). It was pointed out that mutualistic networks are nested (Bascompte & Jordano 2007). Nested subset structure was documented in host-parasite systems (Patterson et al. 2009) facilitation plant networks (Verdu & Valiente-Banuet 2008), ant–plant mutualistic networks (Rico-Gray et al. 2011) and is only at the beginning to be approached in the study of mycorrhizal systems (Southwood et al. 2005, Montesinos-Navarro et al. 2012). Nestedness has an important property; it makes the community more robust against extinction (Memmott et al. 2004). In mutualistic networks competition is relaxed either among host or among mutualists (Bastolla et al. 2009) and has a positive effect on the stability of mutualistic communities (Okuyama & Holland 2008).

Modularity is another feature to be investigated in bipartite networks and it quantifies the extent, relative to the null network model, to which vertices representing species cluster into community groups (Barber 2007). Biological systems are modular in the sense that they are composed of quasi-independent parts that not only are tightly integrated but also exhibit a certain degree of interdependence (Schlosser & Wagner 2004). The modular structure of complex networks plays a critical role in their function (Newman 2006, Guimera & Amaral 2005) meaning that different groups of nodes perform different functions with some degree of independence. The investigations on modularity are of the same category as hierarchical clustering performed with classical clustering algorithms. Modularity was documented for mutualistic networks such as seed dispersal (Donatti et al. 2011, Mello et al. 2011 a,b) plant-pollination (Olesen et al. 2007, Valdovinos et al. 2009, Ramos–Jiliberto et al. 2010) and arbuscular mycorrhizae-plants interactions (Montesinos-Navarro et al. 2012).

Alternative algorithms for testing community structure, based on presence-absence matrices, can be employed in order to have a different perspective or in order to compare them with network analysis results: guild proportionality or nestedness which we have already mentioned (Patterson & Atmar 1986), Diamond's (1975) competition induced checkerboards are methods commonly used to test community assemblage rules. One of the frequently employed indices is C-score developed by Stone & Roberts (1990). It measures the degree to which species co-occur in competition driven communities.

The present paper addresses the topological complexity of the system consisting of several woody species (hosts) and their ectomycorrhizal associates, in a forest at the city edge of the city of Cluj-Napoca, in central Romania. The community structure of ectomycorrhizal macromycetes associated with several woody hosts was investigated using both classical approaches in community analysis (cluster analysis, non dimensional scaling, C-score) and bipartite network descriptors (connectivity, asymmetry, centrality measures, nestedness and modularity).

The study addresses the following issues: (i) the association of the mycobionts with their plant hosts is non-random and nested. Species play different functional roles in the community, (ii) the association is more intimate than mutualistic relationships which have been described elsewhere, a property that can be quantified in terms of network connectivity, nestedness and modularity. The community structure of ectomycorrhizal macromycetes is not competition driven and macrofungal species play different roles within the community, (iii) the network architecture is characteristic of the partnership between trees and shrubs as hosts and ectomycorrhizal macromycetes and is comparable to other mutualistic networks which have been described elsewhere. Network metrics complement the information obtained from other classical quantitative methods.

The analyzed matrix of ectomycorrhizal fungi and their selected list of hosts are considered a metacommunity if hosts are viewed as equivalents to sites to conform to the metacommunity definition as a set of ecological communities at different sites (Leibold & Mikelson 2002).

Network analysis was meant to unravel structural aspects of macrofungal diversity explaining the differences in acquisition of mutualists between tree and shrub species, based on the explanatory power of network metrics.

Materials and methods

Study site

The observations were performed in a typical temperate broadleaved mixed forest in a hilly region managed by the Forestry District Cluj-Napoca, forest production unit IV, known locally as Hoia forest covering 295 ha.

Hoia hill covered by the investigated forest stand reaches altitudes varying in the range of 506-548 m and is situated at 46°46' N, 23°30' E. The annual average temperature oscillates around +8° C, the minimum annual average is recorded in January (from -2° C to +5° C) while the maxima are recorded in July (from +15° C to +20° C). The average annual precipitations are situated in the range 670-1000 mm/m^2. The forest types are characteristic for hilly areas, mainly Transsylvanian *Quercus petraea* and *Carpinus betulus* forests, on clay illuvial brown soils (preluvosoils), with mesophytic graminicolous herbaceous cover. Except for small natural islands of *Quercus pubescens*, the stands are former coppices transformed into high forest, in the range of 55-100 years (Anonymous 1999).

According to functional classification of forest stands, it is considered as recreational forest consisting of a mosaic of stands dominated by *Quercus petraea* (Matt.) Liebl mixed with *Quercus robur* L. or *Quercus cerris* L., stands dominated by *Carpinus betulus* L. and natural stands consisting of *Quercus pubescens* Mill., a thermophilous species forming forest patches in different areas of Transylvania. [At Hoia, on southern slopes, stands with *Q. pubescens* cover 6.2 ha but scattered individuals can be found at he forest edge of other stands on the southern slopes.] Other important woody species with ectomycorrhizae, endoectomycorrhizae and arbuscular mycorrhizae found in Hoia forest are: *Tilia tomentosa* Moench.*, Tilia cordata* Mill.*, Corylus avellana* L*, Sorbus torminalis* (L.) Crantz*, Crategus monogyna* Jacq.*, Rosa canina* L.*, Ligustrum vulgare* L.*, Viburnum lantana* L.*, Sambucus nigra* L.*, Cornus sanguinea* L.*, Euonymus europaea* L.*, Acer campestre* L.*, Fraxinus excelsior* L.*, Acer pseudoplatanu* L.*,* scattered trees of *Fagus sylvatica* L.*, Prunus avium* L. and *Robinia pseudacacia* L. Selected ectomycorrhizal woody species chosen for the current study were *Quercus cerris*, *Q. robur*, *Q. petraea*., *Tilia tomentosa / Tilia cordata*, *Carpinus betulus*, *Corylus avellana* and *Q. pubescens.* Concerning *Tilia* species, the most frequently encountered species is *Tilia tomentosa* considered under the present study as characteristic host for ectomycorrhizal mycobionts.

The forest patch with *Q. pubescens* is a protected area (Work Group NATURA 2000, 2008), with high conservation value due to the fact that it is included in the rare forest and habitat types classified as: 91HO Pannonian woods with *Q. pubescens*, according to NATURA 2000 and 41.7373 intra-Carpathian insular *Quercus virgiliana* woods, according to Palearctic Habitats and R4160 *Quercus pubescens* Dacian forests and woodlands with *Lithospermum purpurocoeruleum* L. according to Romanian Habitats (Doniță et al. 2005). The site covers 8 ha on Southern and South-Western slopes of the Hoia forest, being represented by a mixture of forest and pasture patches, harboring conservation important plant species as *Adonis vernalis* L.*,* *Cephalaria radiata* Griseb. et Schenk.*,* *Stipa pulcherrima* K.Koch*,* *Salvia transsylvanica* (Schur ex Griseb.) Schur.*,* *Centaurea atropurpurea* Waldst. et Kit. and *Viola jooi* Janka.

Data collection

A detailed species list is provided for mycorrhizal macromycetes, the result of surveys between 1999 and 2011, being attached to *Supplementary information*. Nomenclature follows the online Index Fungorum. Only aboveground fructifications were considered in assigning mycobionts. However, the soil inhabiting, cosmopolitan and generalist mycobiont *Coenococcum geophilum* found in all samples containing *Quercus* spp. assimilative roots (Fodor et al. 2011, Şesan et al. 2010) and also associated to other broadleaved species roots investigated during the present study was considered.

Ectomycorrhizal fungi were collected on slopes dominated by *Quercus* spp. and on the forest plateau. Anthropogenic stress is represented in the area by expanding real estate business leading to new constructions placed near the forest edge, overexploitation due to the fact that many forest areas are now private properties, the pressure of week-end tourism and grazing by sheep and cows.

Network construction

The observations were organized in an adjacency matrix of presence/absence data, containing species of plants (woody host species) and ectomycorrhizal macrofungi. The proposed ecological network is a bipartite (2 mode) mutualistic network containing trees such as: *Quercus cerris*, *Q. robur*, *Q. petraea*, *Tilia cordata*, *Carpinus betulus*, *Corylus avellana*, *Q. pubescens*. The second group of the bipartite network is represented by ectomycorrhizal macrofungi with aboveground carpophores, with the one exception, being the ubiquitous and underground forming sclerotia, *Coenococcum geophilum* Fr. The network was constructed for the analysis of direct, pair-wise interactions and was based on a presence/absence community matrix considered as the fundamental unit in community ecology and biogeography (McCoy & Heck 1987). It was used also for the calculation of several characteristic community indices (C-score, nestedness) where hosts stand for distinct sites and associated mutualistic mycorrhizal fungi, for local communities.

Network metrics and ectomycorrhizal community structure assessment

For the detection of community structure, several network specific metrics were employed (node degree listing, connectance, link density, network diameter and size, node degree, betweenness, closeness centrality and node centralization) several classical community structure metrics in network context (nestedness and modularity) and classical structure assessment metrics such as C-score and cluster analysis and non metric multidimensional scaling.

Node degree (D_i) is the number of edges per vertex. Node degrees are summarized in the adjacency matrix which is the same with community matrix. Node degree is considered also a measure of centrality (Scotti et al. 2007)

Connectance (C) is a global net index and quantifies the realized number of links per network. In bipartite networks it is calculated as:

$$C = \frac{L}{I \cdot J} \tag{1}$$

where L stands for realized links, I and J represent the number of species in each party of the bipartite network (J for higher trophic level party, ectomycorrhizal species in the present case). It is one of the simplest and most commonly used metrics to describe the density of links in a network and it is interpreted as the degree of generalization with consequences for community stability (May 1972, Dunne et al. 2002).

As sampling was performed over a relatively long period of time, the bias of undersampling (Blüthgen 2010) was significantly diminished.

Web asymmetry evaluates the balance between the two levels of the bipartite graph (Blüthgen et al. 2007):

$$W = \frac{J - I}{J + I} \tag{2}$$

Positive numbers indicate higher trophic level species while negative numbers indicate lower trophic level species prevalence. The index scales within the interval [-1; 1].

Link density is defined by the number of links in a network and is calculated as the ratio of links number by nodes number.

Centrality in a network is a function of node degrees and of the frequency with which a node falls between other two points on the shortest (geodesic) path connecting them. Centrality of a node (or the role / position of the node in the network) can be referenced by any of three quantities: node degree, betweenness and closeness (Freeman 1979). Nodes with central position exert control on the network and communicate with other nodes within a minimum of distance.

Betweenness centrality of a vertex k is a number of shortest paths or geodesics between pairs of other vertices that run through the vertex k.

$$B_i = \sum_{i>k}^{n} \sum_{j>k}^{n} b_j \, (p_k) \tag{3}$$

The number of equally shortest paths between vertices i and j is represented *by bij*. The symbol, p_k stands for the node k and n for all other nodes of the graph. Nodes with high betweeness control the network.

Closeness centrality measures how close to a focal vertex is to all other vertices in the network considering the geodesic distances or shortest paths of the focal node to all other nodes in the graph:

$$C_i = \sum_{j=1 i \neq j} \frac{d_j}{n-1} \tag{4}$$

The independence of a node is described by its closeness to all other nodes in a graph (Freeman 1979).

Degree centrality is the simplest form of centrality and it assesses the importance of a node according to the normalized degree in the interaction network (Gòmez & Perfetti 2011). The normalized version divides simple degree by the maximum degree possible, a measure ranging from 0 to 1.

Network diameter is the maximal distance between any pair of its vertices and it is a measure of the cohesion of the network.

Network size M was calculated as:

$$M = F \cdot P \tag{5}$$

where F stands for total number of vertices corresponding to fungal ectomycorrhizal species and P for number of vertices corresponding to plant species.

Modularity of an ecological network is a signature of heterogeneous link distribution (Olesen et al. 2007) modules are composed of species having many interactions among themselves and few interactions with species from other modules. It is the degree of species organization into densely connected modules, a surrogate for guild structure (Mello et al. 2011 a). Modules can be detected at topological level, at the smallest scale being defined as subgraphs. The methodology is based on node connectivity surmising that nodes are connected according to their role in the network (Guimera & Atmar 2005). There are several algorithms proposed to optimally separate modules: simulated annealing (Guimera & Atmar 2005) or spectral properties of the network (Newman 2006). In the present study the algorithm of simulated annealing which is a Monte Carlo procedure provided by Guimera & Atmar (2005) and incorporated in the software NETCARTO, was employed.

Modularity was calculated, according to the equation:

$$Q = \sum \left[\frac{ms}{m} - \left(\frac{ds}{2m} \right)^2 \right] \tag{6}$$

where: Q stands for modularity, ms represents the number of links in module s, ds represents the sum of degrees k_i of the vertices in the module s, m stands for the number of links in the neywork. It is worth to mention that modularity, as the amount of clustering based on network connectance, dictates the basic buiding blocks of the network (Olesen et al. 2007)

Given a partition of a network m in community, the aim is to improve the partition by computing a new one with a high degree of modularity. Given a partition of a network one can improve the partition by computing a new one with a higher value of modularity. The identification process of modules consists of maximizing the network modularity by simulated annealing (a stochastic optimization technique which enables one to find the low-cost configuration in the network). It enables the operator to perform an exhaustive search without an *a priori* specification of the modules number. It is hence plausible to consider that nodes in the network are connected according to their roles. It must be stressed that modularity is a global index addressing whole network. Guimera & Amaral (2005) suggest that the global role of nodes assessed by modularity is a better indicator of their importance than the node degree. The rationale of the index dwells in minimizing the number of links between modules and maximizing the number of links within modules. It is recommended that the network be tested repeatedly. The need for repeated runs is dictated by the heuristic nature of the algorithm (Fortuna et al. 2010). Topological properties of the nodes can be employed to define roles: these are participation coefficient and within module degree *z*.

The role of a node is assessed using the participation coefficient which is also a measure of connectivity among modules (Olesen et al. 2007) and defines how a node is positioned within its own module and with respect to other modules (Guimera & Amaral 2005). The coefficient is calculated for each node. It defines how well distributed the links of a node are among different modules according to the equation:

$$P_i = 1 - \sum_{S=1}^{Nm} \left(\frac{k_{is}}{k_i} \right)^2 \tag{7}$$

where: k_{is} represents the number of links node i shares with other nodes in module s_i, k_i stands for the degree of node i and Nm stands for number of modules. The index takes values in the range 0 and 1: 0 means that all links are within a given module and 1 that all links are distributed uniformly among modules.

Within module degree z is a descriptor derived from modularity assessment which measures how well a node is connected to other nodes in the module: it distinguishes the hub from non-hub nodes and is calculated according to the equation (Guimera & Amaral 2005):

$$Z_i = \frac{k_i - k_{si\_mean}}{\sigma_{si}} \tag{8}$$

where: k_i stands for the number of links of node *I* to other nodes within own module s_i, $k_{si\ mean}$ stands for the mean over all nodes in module *si* and σ_{si} is the standard deviation of *k* in s_i. High values of z_i indicate high within module degree and accordingly an important role. Nodes with $z \geq 2.5$ are classified as module hubs (highly linked to other nodes) and nodes with $z < 2.5$ are classified as non-hubs. Hub and non-hub nodes can be further characterized using participation coefficient values. Within z = P parameter space 7 regions are delimited according to the roles palyed by the nodes. The non-hub nodes can be partitioned among four different regions: *R1* contains ultra-peripheral nodes, nodes with all their links within module at $p \leq 0.05$, *R2* contains peripheral nodes with most of the links confined to their module with $0.05 < p \leq 0.62$, *R3* contains non-hub connector nodes with many links to other modules with $0.62 < p \leq 0.80$ and *R4* contains non-hub, kinless nodes with links distributed among all modules. The other three regions conyain hub modules: *R5* that contains provincial hubs with most of their links within own hub with $p \leq 0.30$ and *R6* that contains connector hubs with many links to other hubs with $0.30 < p \leq 0.75$ and *R7* containing kinless nodes with links distributed homogenously among hubs ($p > 0.75$).

Nestedness is a community descriptor which can also be employed as network descriptor because in both situations a presence / absence matrix is employed. It depicts a particular type of asymmetry in interactions. The method quantifying the nestedness was first employed in biogeography to quantify the degree in which smaller islands represent a subset of species found in larger ones. This pattern was defined as nested and represented by a triangular shape of the distribution of ones in the adjacency matrix after rows and columns have been reordered by increasing number of links. The calculation was performed using the most popular temperature estimator proposed by Atmar & Patterson (1993). This index is constructed using the median line in the ranked adjacency matrix, a null model provided for comparison with observed data. This line equally separates holes and full cells in the matrix (zeros and ones). The ”temperature” is a measure of the dispersion of holes with respect to the median.

Nestedness was calculated as $N = (100\text{-}T)/100$ in which *T* is the matrix temperature, a measure of how the presence / absence pattern departs from perfect nestedness. *T* calculation was performed with software Binmatnest (Rodríguez-Gironés, & Santamaría 2006). A genetic algorithm was employed by the authors to calculate the temperature specifying a population size (30 possible solutions with the best selected for subsequent variation), a tour size of 7 as recommended by authors, and 2000 generations. This metric depends on the matrix size meaning that larger matrices are more reliable in assessing nestedness (Ulrich & Gotelli 2007). Two null models were run using simulated matrices which preserve the marginals from the observed matrix. Null models are pattern generating models based on randomization of ecological data (Gotelli & Graves 1996). The models answer to the question whether the observation data appear non-random when compared to simulated data meaning that randomization produces a pattern that would be expected in the absence of a particular process. The approach, initially largely used in biogeography resembles hypothesis testing in conventional statistics.

In some respects, nestedness is testing the same thing as Cscore, however, C score is a better descriptor of species communities assembled by competition by considering the checkerboard model presumably generated by competition as defining community structure.

Interaction richness is analogous simply the total number of links in the network (Tylianakis et al. 2007).

The unipartite projection of the bipartite graph (Gómez & Perfetti 2011) was generated considering links which depict shared mutualists among trees. That is, in the unipartite version, two tree species are linked and weighted by shared ectomycorrhizal species and another representation links fungal species according to their connections to hosts. The unimodal projection of fungi was employed for the calculation of betweeness, closeness and normalized degree centrality since most of network descriptors are defined for those (Borgatti & Everett 1997, Olesen et al. 2007). Unimodal projections can be particularly useful in mapping community but the information loss associated with the transformation is inevitable (Padrón et al. 2011). The bipartite and unipartite networks were analyzed and graphically generated with and Pajek software (Batajeli & Mrvar 2010).

Modularity was assessed using the software NETCARTO. Modules were generated in Pajek.

The significance of patterns in null models are tested using randomization tests: describe a pattern by a single index then compare the observed value of the index to the distribution of index values from simulated matrices (Manly 1991, Gotelli & Entsminger 2001). The randomizations for the tested indices, co-occurrence, nestedness and modularity were performed by the programs used.

Additional community structure assessment: Co-occurrence, similarity

Species co-occurrence function of shared (or not shared) hosts was tested using one of the most reliable co-occurrence indices, C-score in order to find whether assemblage of the ectomycorrhizal community was random or assembled by interspecific competition (Diamond 1975). A null model considering random species co-occurrence is tested on a large number of null communities, usually 1000. The position of the observed index in the frequency distribution of simulated data is then used to assign a probability value to the pattern (Manly 1991, Gotelli 2001). Both metrics were calculated using Ecosim7 software (Gotelli & Entsminger 2001). The C-score is the average of all possible checkerboard pairs, calculated for species which occur at least once in a presence / absence matrix. In competitively structured communities or structured by some other interaction type the C-score should be significantly larger than expected by chance (Gotelli & McCabe 2002). A standardized effect size (SES) is calculated: a value greater than 2 and lesser than -2 is statistically significant with a tail probability less than 0.05 and stands for a significance test for accepting or rejecting the null hypothesis (of random species assembly). The calculated SES uses z-transformed scores of the original data and can be employed to compare results from different matrices and algorithms (Gotelli & Mc Cabe 2002).

In order to assess similarities between woody species in terms of ectomycorrhizal associates, several similarity indices were tested and the final decision was taken as function of the best cophenetic correlation result (Legendre & Legendre 1998). The Kulczynski similarity index yielded the best results, with cophenetic correlation of 0.8189. Similarity analysis in terms of shared ectomycorrhizal species by seven woody species was performed using pair-wise clustering algorithm. For a better understanding of similarity distances among host species in terms of ectomycorrhizal mutualists, two dimensional non metric multidimensional scaling was employed as ordination algorithm; the Kulczynski similarity index $[2C/(N_1+N2-2C)$ with C = common species of site $N1$ and $N2]$ was the best choice for the ordination yielding the lowest stress of 0.163. Values around 0.1 are considered appropriate for goodness-of-fit test (Borgatti & Everett 1997). The calculations and graphical representations were performed using the software PAST (Hammer et al. 2001).

Results

The generated network is an undirected, unweighted and qualitative bipartite graph depicting the mutualist relationships between trees and ectomycorrhizal macrofungi (fig. 1). The topology analysis and C score result reveal the non random assemblage of the network of trees and ectomycorrhizal macromycetes; the network is asymmetric, highly connected, nested and modular.

The descriptors displayed in Table 1 are size dependent and are a good background for the comparison with other mutualistic networks described by different authors.

The network (Table 1) is characterized by large size (609 potential links) and also its high connectance (0.42), unusually large as compared to other mutualistic networks: plant facilitation networks (0.24), described by Verdù and Valiente-Banuet (2008), pollination networks, about 0.043-0.070 (Ramos-Jiliberto et al. 2010), 0.11 (Olesen et al. 2006). 0.086 (Hegland et al. 2010), 0.043 to 0.070 (Ramos-Jiliberto et al 2010), 0.15 and 0.24 (de Mendoça Santos et al. 2010) or 0.026 (Petanidou et al. 2008) but comparable with plant pollination networks published earlier such as 0.40 in bog plants and their pollinators (Douglas 1983) or hummingbirds as pollinators and plants in Colombia (Snow & Snow 1980). High connectance is explained by the low number of considered hosts, previous studies showing that connectivy decreases exponentially as the number of hosts increases (Poulin 2010).

It is currently considered that low connectance indicates highly specialized communities (Dyer et al. 2010), the ectomycorrhizal network indicating the opposite at the level of woody species group (average node degree of 29.57). Trees acquire a great number of ectomycorrhizal partners during their

Table 1 Network metrics of the bipartite graph depicting links between forest tree species in the Hoia recreational forest, of the city of Cluj and ectomycorrhizal fungi

Network summary	Trees-ectomycorrhizal fungi mutualistic network (94 vertices, 246 links)
Interaction richness = number of links	246
Species richness = number of nodes	7 host species, 87 mycobionts
Connectance	0.42
Richness ratio	12
Web asymmetry	0.85
Network size, M	609
Bipartite network diameter	4
Average distance between reachable pairs	2.47
Average link density	2.63
Average node degree	29.57 for hosts 2.63 for mycobionts
Whole network average node degree	5.106
Statistics for closeness centrality (unipartite network of ectomycorrhizal fungi)	min = 0.6277; max = 1, mean = 0.810 ± 0.1160
Statistics for betweenness centrality (unipartite network of ectomycorrhizal fungi)	min = 0; max = 0.0048; mean = 0.00019 ± 0.0022
Statistics for normalized degree centrality (unipartite network of ectomycorrhizal fungi)	min = 0.4069; max = 1; mean = 0,8202 ± 0.1655

life time sharing these species. Hosts with the largest numbers of ectomycorrhizal partners expressed as node degree are *Quercus petraea* (68) and *Carpinus betulus* (46). It is currently considered that generalists maintain the stability of a network (Diaz - Castelazo et al. 2010). Specialists have lower node degree than generalists (Dormann 2011), many macromycetes being linked to one, two or three tree species (average node degree = 2.63). All considered hosts are generalists while almost half of the identified mycobionts are specialists, a characteristic of the described ectomycorrhizal network.

Low network diameter (4) differs from reported diameters of pollination networks between 7 and 8 (Petanidou et al. 2008) sustaining high cohesion of the web. The network presents high asymmetry (0.85), with the prevalence of the higher trophic level species, the ectomycorrhizal fungi.

For the few selected tree species there are many mycobionts, the ratio of tree species to ectomycorrhizal fungi (richness ratio) is 12.42, also an indication of asymmetry. For trees, node degree depicts the actual number of mycobionts functioning as a proxy for species richness. For ectomycorrhizal fungi, node degree separates mycobiont generalists versus specialists in what concerns the number of hosts. The maximum number of associated hosts (also maximum node degree) is 7 for ectomycorrhizal fungi. The average distance between reachable pairs is small, 2.47, a common characteristic for mutualistic bipartite networks (Bezerra et al. 2009).

In the unipartite network version centered on macromycetes (not illustrated), 49 fungal species display betweeness centrality, BC > 0 playing the role of connectors (Gonzales et al. 2010), connecting areas of the network otherwise sparsely linked. They are generalist species important for the cohesiveness of the network and account for 56.32% of the species in the network, remarkably higher representation than in seed dispersal networks, 11.9% (Spotswood at al. 2012) but close to plant-pollination networks as 57% (Inoue and Pyke 1988)). Examples of ectomycorrhizal fungi playing the role of connectors are: *Boletus chrysenteron* Bull*, Hebeloma crustuliniforme* (Bull.) Quél*, Tricholoma virgatum* (Fr.) P. Kumm*, Boletus aestivalis* (Paulet) Fr.*, Laccaria laccata* (Scop.) Cooke*, Amanita pantherina* (DC.) Krombh, *Boletus edulis* Bull.*, Coenococcum geophilum* Fr.*, Amanita phalloides* (Vaill. ex Fr.) Link*, Russula cyanoxantha* (Schaeff.) Fr.*, Lactarius. piperatus* (L.) Pers*, Russula foetens* (Pers.) Pers., and others. *Coenococcum geophilum* is the most frequently identified species on roots being responsible for linking different hosts in a mycorrhizal network (Valentine et al. 2004).

The remaining 38 fungal nodes are pending, being isolated and connected to just one host and are to be considered ultra-peripheral. However, the largest participation in terms of betweenness centrality is demonstrated by 24 fungal species (0.0048). All nodes display large values for closeness centrality (CC extreme values: maximum of 1 for the same 24 fungal species as for betweenness centrality and minimum of 0.6277 for *Boletus edulis*). Among mycobionts with high closeness centrality (CC) values are *Coenococcum geophilum, Amanita phalloides, Lactarius piperatus, Lacaria laccata* and *Hebeloma crustuliforme*. The highest normalized degree signifies the highest linking capacity for 24 fungal species (maximum value of 1), same species as for betweenness and closeness centrality.

The unipartite projection shows that all selected woody species are linked by ectomycorrhizal mutualists, their network is completely connected; connectance = 1, a situation described for several pollination networks and parasite – metazoans networks (Poulin 2010). The unipartite projection centered on hosts is a surrogate for niche overlap, highest number of links between hosts reflecting the level of mutualist share among woody species (fig.1).

Nestedness analysis shows a highly sig-

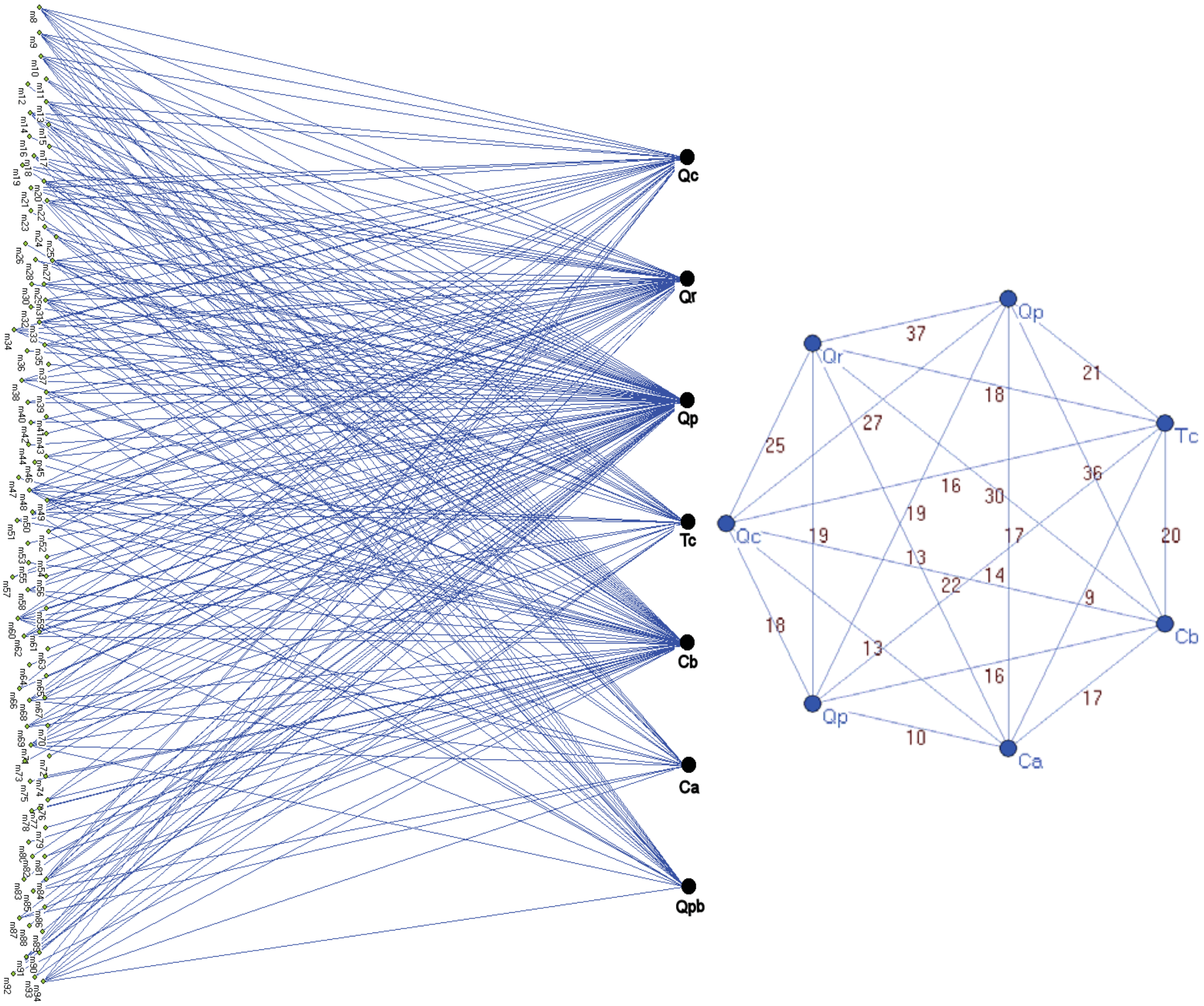

Figure 1 On the left, bipartite network of main woody species and ectomycorrhizal associates in broad-leaved mixed forest, Hoia recreational forest, Forestry District Cluj-Napoca. On the right, the unipartite version of the same network. Notations: Qc - *Quercus cerris* L., Qr - *Q. robur* L., Qp - *Q. petraea* (Matt.) Liebl., Tc - *Tilia tomentosa* Miller, Cb - *Carpinus betulus* L., Ca - *Corylus avellana* L., Qpb - *Q. pubescens* Mill. Fungal partners are listed in the appendix. Figures attached to unipartite graph represent the number of shared ectomycorrhizal species

nificant difference of the observed matrix temperature as compared to null model I and II simulated matrix temperatures (T = 16.78, mean simulated T for null model I = 38.29, mean simulated T for null model II = 31.63) N = 0.83, corresponds to relatively high nestedness of the ectomycorrhizal network. It implies also a higher nestedness degree for the observed matrix as expected from the null model runs. The nested matrix (Fig. 3) illustrates the deviation from random pattern and the closeness of the observation data to a perfectly packed array of presence / absence cells. The final pattern after re-arrangements of the matrix rows and columns is with most of the interactions mapped in the lower half of the matrix. Nested patterns typically yield a core of species (generalists) as a cluster for other peripheral species, showing a structured architecture compared to random networks.

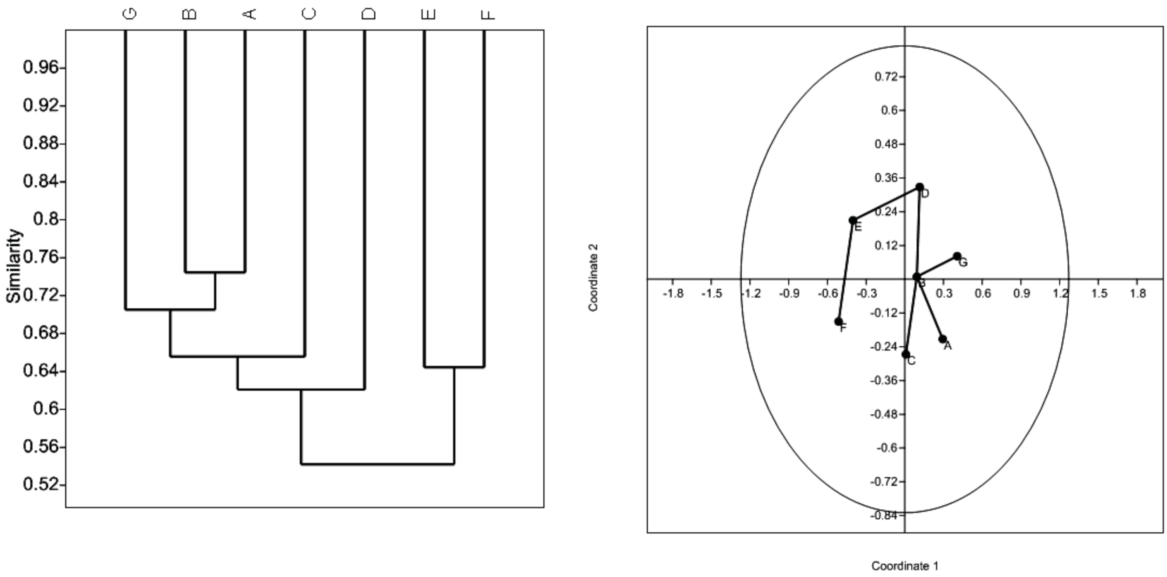

Figure 2 Left, cluster ordination using Kulczynski similarity index and pair-wise algorithm. Right, two dimensional non metric multidimensional scaling ordination with minimum spanning tree distances among hosts in terms of ectomycorrhizal partners: A - *Quercus cerris*, B - *Q. robur*, C - *Q. petraea*, D - *Tilia tomentosa*, E - *Carpinus betulus*, F - *Corylus avellana*, G - *Q. pubescens*

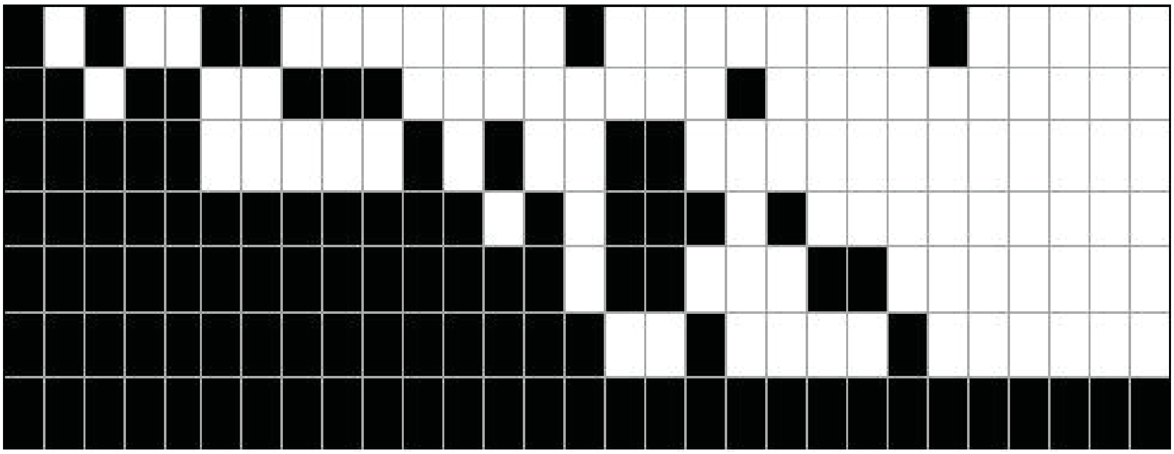

Figure 3 Nested, packed adjacency matrix of the bipartite network (trees-ectomycorrhizal macrofungi)

The nestedness as a community property in the ectomycorrhizal bipartite network displays similar trend which are comparable to other mutualistic networks such as plant facilitation network-0.876 (Verdú and Valiente-Banuet 2008), seed dispersal - 0.843 or pollination networks - from 0.853 to 0.982 (Bascompte et al 2003: Petanodou et al. 2008), cleaning mutualist networks, 0.82 (Sazima et al. 2010) or ectoparasite-vertebrate networks-from 0.48 to 0.97 (Graham et al. 2009). It is commonly interpreted as specialization asymmetry: specialists (species with few links, ectomycorrhizal fungi in this case) interact with generalists (species with many links, woody hosts in this case) (Blüthgen et al. 2008).

On the other hand, host specificity must be taken into consideration as a factor affecting the extent of nestedness, previously illustrated for host-parasite interaction networks (Patterson et al. 2009). This property mirrors network asymmetry with generalist species interacting with other generalists as well as with specialists and specialists displaying few links generally with generalists from the other network group (Graham et al. 2009). However, the association with only one host in the case of ectomycorrhizal networks is questionable as being determined by specialization since there are multiple possibilities for same fungal species being associated with other woody species not considered here.

Modularity analysis yielded four modules that were identified after running the NETCARTO package on the original presence / absence matrix, using repeated runs (between 50 and 100 randomizations). The highest value obtained for modularity index reported is (Q = 0.2417), together with the model that minimizes the number of links between modules. The mean of the simulated index by repeated randomizations is significantly higher than the observed index (0.2643 ± 0.0056). There are 25 species in first module including *Carpinus betulus*, 28 species in the second module including *Quercus petraea*, 18 species in the third module including *Quercus robur*, and 23 species in the forth module including *Quercus cerris*, *Tilia cordata, Corylus avellana* and *Quercus pubescens* (Fig. 5). A modularity index of 0.2417 indicates low modularity of the bipartite network, many links being externalized among modules instead of being maximized within modules also many nodes are pending, a situation favorable for linkage to other potential hosts not included in the present study.

For comparison, pollination networks display at average 8.8 modules (Olesen et al. 2007) seed dispersal network display 4 to 5

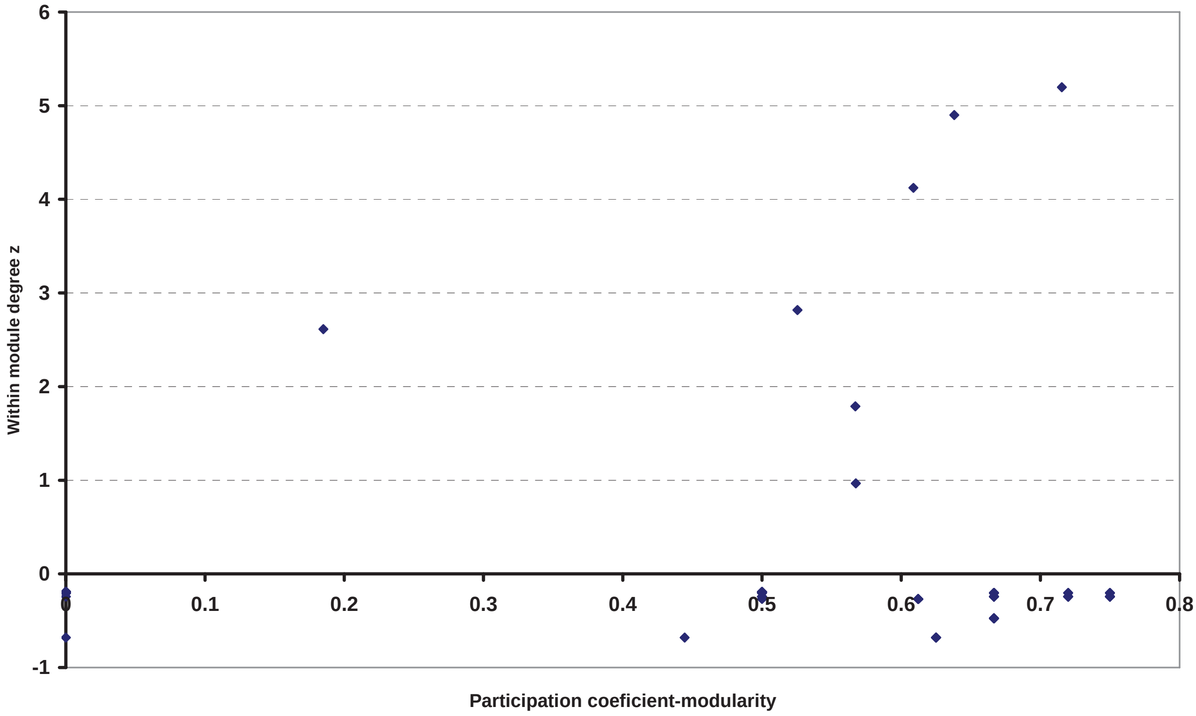

Figure 4 Participation coefficient-within module degree z space (classification of nodes according to their roles) representation of the bipartite mutualistic network: ectomycorrhizal fungi-woody hosts in Hoia forest

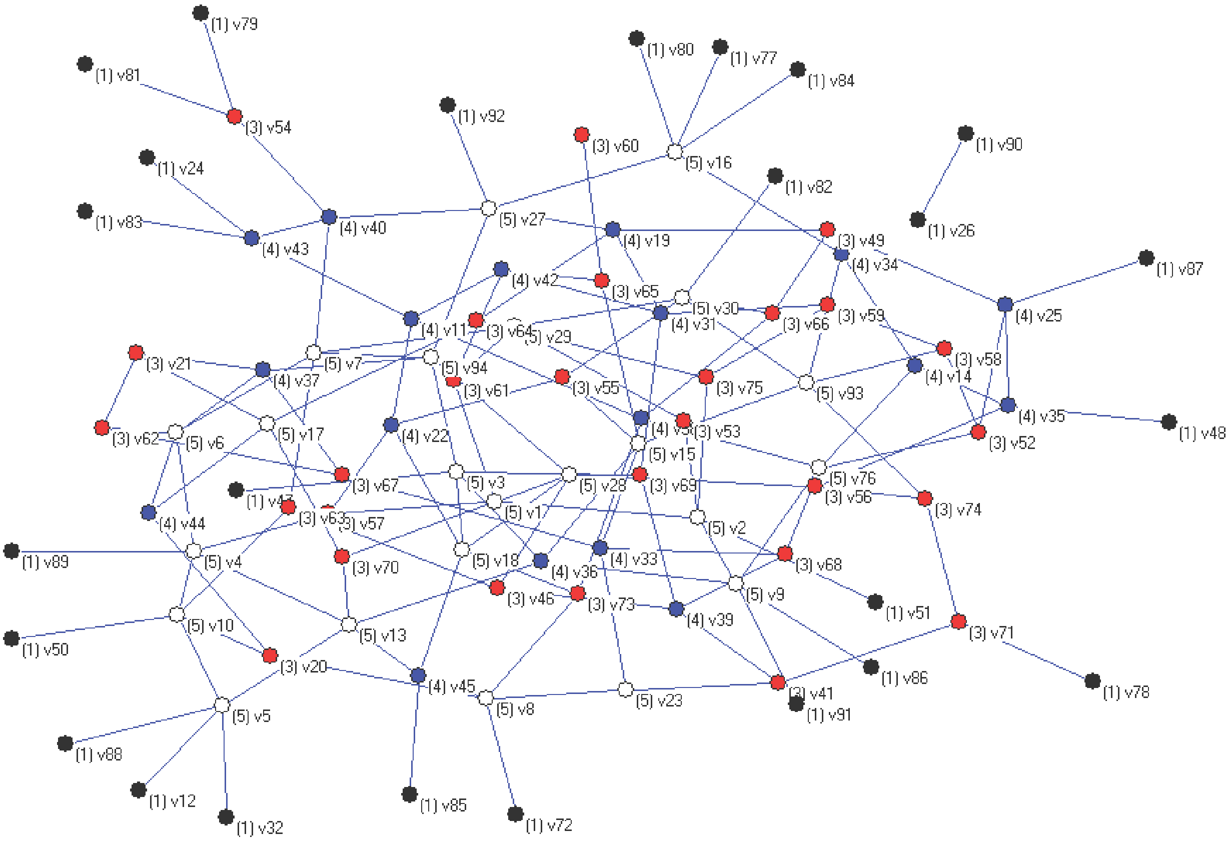

Figure 5 Partition of the bipartite network (ectomycorrhizal species - woody hosts) in 4 modules; members of the same module are depicted in the same color and the number of the corresponding module in brackets

modules and modularity between 0.20 and 0.44 (Mello et al. 2011 b). According to Guimera and Amaral (2005) classification (Fig. 4), taking into account the low participation coefficient and z there are 38 nodes in R1 category (ultra-peripheral) such as *Phallus impudicus, Russula pseudointegra, Amanita battarae, Lecinum carpini,* 9 nodes are from R2 category of peripheral nodes (*Boletus appendiculatus, Cratarellus cornucopioides, Hebeloma crustuliforme* for instance) and 40 nodes are from R3 category of non-hub connectors meaning that approximately 42% of the nodes display many links to other modules (*Boletus edulis*, for instance.). Network hub nodes (*Quercus cerris, Quercus robur, Quercus petraea* and *Carpinus betulus*) are included in R6 region of connector hubs ($0.30 < p < 0.75$) characterized by many links to other modules (Figs. 4 & 5). *Quercus pubescens* is included in R5 region playing the role of a provincial hub while *Tilia cordata* and *Corylus avellana* are paced in the non-hub region R2 of peripherals (Figs. 4 and 5).

The results are comparable with those reported for other types of mutualistic networks; Q = 0.22 in pollination network (Bezerra et al. 2009): from 0.474 to 0.711 in complex pollination networks (Saavedra et al. 2008); 0.551, 0.771, 0.653 in plant facilitation networks (Saavedra et al. 2008): 0.422 (Donatti et al. 2011) and 0.45 (Mello et al. 2011b) in seed dispersal network. Host-parasites networks display a large variation of the modularity index: from 0.16 to 0.49 (Krasnov et al. 2012).

Combining the information from centrality analysis and modularity (Table 1 and Fig. 4) demonstrates that that nodes with highest closeness, betweenness and normalized degree centrality are highly connected and can be superimposed on R2 region (peripherals) also on R3 region of non-hub connectors. Within R2 module, species are tied together, a trait which is of main importance in maintaining network cohesiveness (Jordano 2010): therefore the species are close one to another in terms of network architecture (closeness centrality).

C-score. Testing the hypothesis of a competition assembled fungal community gives the expected result, there is no significant difference between the observed C- score and the index simulated by randomizations, (observed index = 0.5961, mean simulated index = 0.5858. SES = 0.2602). The presented network describes the ectomycorrhizal community assembled by different mechanisms, competition playing a secondary role.

Hierarchical clustering and non-metric dimensional scaling show that there are 2 distinct clusters or groups. One cluster merges *Corylus avellana* and *Q. pubescens* and the second cluster merges the remaining host species (Fig.2) Minimum spanning tree applied to non-metric dimensional scaling segregates as the hosts in two groups: *Corylus avellana* and *Carpinus betulus* are merged in one group and the rest of the hosts, in the other group. The most distant in terms of path length are *Corylus avellana* and the group merging *Q. cerris, Q. petraea* and *Q. pubescens*. However, according to the modularity analysis, there are 5 hub and 2 non-hub nodes corresponding to the hosts that are packed within the four modules. The group formed by *Carpinus betulus* and *Corylus avellana* is not homogenous in terms of the functional roles since *Carpinus betulus* plays the role of a connector hub while *Corylus avellana* is a non-hub peripheral node. *Quercus pubescens* is closer in distance terms to *Quercus robur* and *Quercus petraea* which are connector hubs but it plays the role of a peripheral hub. The explanation for these differences in group or module identification algorithms resides in the fact that the resemblance space characterizing hierarchical clustering and ordination methods is different from z-P space defined in terms of connectance. In non-metric multidimensional scaling the distances between resembling entities are scaling with the degree of similarity while in networks the distances are measured as length of paths between nodes or connectance. The role of a species in the network depends on the number of interactions it establishes, some species interact heavily only with species from their own module while other species show extremely generalized interactions something that cannot be depicted by cluster analysis or other ordination methods where all the species are considered equivalent.

Discussion

Network analysis provides deeper insights in the community structure and species interactions using the information contained in presence-absence matrices considered to be less informative than abundance matrices due to the equal weight given to absences and presences in classical community ecology (Legendre & Legendre 1998). Ectomycorrhizal community together with assigned hosts presents all the characteristics of mutualistic network architecture and is coherent (Liebhold and Mikelson 2002) meaning not random as judged on the basis of nestedness and modularity descriptors, highly asymmetric and almost half of the mycorrhizal fungi play the role of tree connectors in the network. All host species are super-generalists while the ectomycorrhizal species group is a mixture of generalists and specialists: generalist species are vital for the network structure, functioning and resilience (Gonzales et al. 2010) because they are not limited by resource or partner availability (Blüthgen et al. 2007) while specialists make a better use of resources or partners. The network is also highly heterogeneous; generalists form a core consisting of few species displaying many links while many species display few links, unlike random networks which in contrast, have a more even distribution of links (Jordano et al. 2003). Hosts (trees and shrubs) playing the role of super-generalists function as hubs for ectomycorrhizal mycobionts in the network adding the interactions that connect different modules (Jordano 2010).

The ectomycorrhizal community is characterized by relatively high connectance, high nestedness and low modularity, a combination of network properties stressed by other authors as a general trait for mutualistic networks (Fortuna et al. 2010, Olesen et al. 2007). The property of high heterogeneity (uneven distribution of node degrees), contrasting with more even distribution in random networks indicates that the network is robust to random disturbances but sensitive to directed losses of nodes (Albert et al. 2000). High connectance is apparently linked to low network size, a property reported previously for plant-pollinator networks (Olesen & Jordano 2002). This is the explanation for the organizational characteristic of any mutualistic network around a core of generalist species that can be reasonably robust to disturbances directed randomly (Jordano 2010).
The nested structure of ectomycorrhizal communities relaxes competition as it was previously observed in pollinator / plant systems (Bastolla et al. 2009: Ramos-Jiliberto et al. 2010) favoring coexistence. The basic idea stressed by this study is that the ectomycorrhizal macrofungi species pool contains subsets which are nested, the dominating tree species harboring the most species rich subset of mutualists. The community assembly is not driven mainly by competition (as in checkerboard model) but by some other mechanisms that generate the nested model.

Network architecture is dominated by high numbers of ectomycorrhizal fungi and low number of the host species, a characteristic encountered in cleaning mutualist assemblages in coral reefs (Guimarães et al. 2006) as the richness species ratio (number of fungal species/number of woody host species) is high, equal to 12.42. This trait affects the degree of nestedness considered to be high in cleaning mutualistic assemblages and also in ectomycorrhizal network, compared to other plant-animal assemblages of similar species richness, mutualistic networks which show less marked patterns of nestedness (Guimarães et al. 2006).

Centrality measures and modularity work together in clarifying the roles of species within the ectomycorrhizal fungi community. Modularity analysis is a finer tuned tool in the assessment of species roles than betweenness centrality (*BC*). Species with $BC > 0$ considered connectors in centrality space, are include in different categories according to participation coefficient-z score space: low z and high participation coefficient (C) place the species in connector R3 region while species high in both C and z scores high are super-generalist species or network hubs (the seven host species). There are 40 connector species which can be considered generalists and 38 ultra-peripheral macromycetes which can be considered specialists and only 9 peripheral species. However, species roles can change in a larger species richness context if additional data on ectomycorrhizal morphotypes and species identified by molecular tools are collected. A low level of modularity in ectomycorrhizal mutualistic network is explained by the high intimacy of the interaction, a trait which affects network architecture in a similar way as in plant-animal mutualistic networks (Fontaine et al. 2011).

The cause of so many mutualists associated with same host is partially explained by insurance hypothesis (Hooper at al. 2005). An alternate explanation comes from graph theory consisting in the property of the preferential attachment of new nodes to an existing network where densely connected nodes tend to acquire more links, colloquially rendered by the expression ”rich get richer” (Barabasi & Albert 1999, Jordano et al. 2003). *Quercus petraea* is a dominant, climax species in the hilly mixed broadleaved forests therefore it acquires many mutualists (68 ectomycorrhizal species). The second species in terms of associated mycobionts (46 species) is hornbeam (*Carpinus betulus*) which is currently replacing the dominant *Quercus* species as a consequence of the interplay of several natural and anthropogenic factors..

The interactions within mutualistic networks are long termed when compared to interactions occurring in food-webs; mutualistic networks are more nested than trophic networks (Thébault & Fontaine 2010) also more connected. In fact, larger mutualistic networks were shown that were both nested and modular also, nestedness being complementary to modularity (Olesen et al. 2007). As connectivity increases, less specialization is expected to characterize the nodes (species) and modularity decreases since this network property depicts the degree of specialization. An ectomycorrhizal network is highly connected due to the high representation of macromycetes generalists. Having a nested structure, the network is highly asymmetric and there is a core of species with a high interaction density, separating two categories: generalists versus specialists. Generalist plant species tend to interact with generalist macrofungi. Rare ectomycorrhizal fungi (for example, *Amanita battarae*) tend to interact with generalist plants gaining greater chances for survival.

The degree of intimacy is higher in ectomycorrhizal networks than in pollination or facilitation networks. It is worth to stress the fact that nestedness is in closer association with mutualistic interactions such as pollination networks (Genini et al. 2010) and plant-ant networks (Guimarães et al. 2006) which are non-intimate mutualistic relationships than modular networks which are associated with antagonistic communities and intimate mutualism (Fontaine et al. 2011). Both nestedness and modularity provide benefits for communities (May 1972, Bastolla et al. 2009). The supergeneralist species (the trees in ectomycorrhizal network) are hubs and connect different modules whicht is a characteristic pattern in mutualistic webs (Jordano 2010)

Modularity is a global level topological property of a complex network and it reveals in the case of ectomycorrhizal network the relationships among trees mediated by mycorrhizal fungal species. Modularity analysis shows that this system is weakly modular: compared to other published mutualistic bipartite networks, the value of the calculated woody species-ectomycorrhizal fungi bipartite network modularity index (0.2417) is small.

Hierarchical clustering results produced two main clusters while modularity assessment produced four distinct modules where nodes were affiliated according to their roles in z-P parameter space. In the case of clustering, the affiliation of species to clusters is performed according to the similarity among woody species in the way they share mycobionts within the resemblance space. Clustering and non-metric dimensional scaling produced similar results: there are two main groups of clusters of host species separated by similarity (clustering) or distance (non-metric dimensional scaling) in terms of ectomycorrhizal mutualists. When considering the modular structure of the network, the hosts are included in different modules and play different roles. Two host species are non-hub peripherals (*Tilia cordata* and *Corylus avellana*), one host is a provincial hub (*Quercus pubescens*) and the other four remaining hosts play the role of connector hubs. However, they are placed in different clusters or groups according to their degree of similarity in sharing mutualist fungi. Modules reflect in a more accurate way the structure of the ectomycorrhizal community in the context of the mutualist relationship with their woody hosts given the possibility to identify the roles played by the species.

The ectomycorrhizal community displays particular structural features not confirming competition hypothesis of the community assembly. The assembly model is not a checkerboard as assessed by C-score since the result show that ectomycorrhizal fungi are not partitioned according to this model in a random manner as function of their hosts which also means that competition is not the main driving force in community shaping. A better result was obtained assuming that fungal mutualistic community is assigned to hosts according to the nested model of community assembly.

It is worth mentioning that nodes which are highly connected or central are easy targets in case of perturbations (Jordan & Scheuring 2004) and the extirpation of these nodes affect the properties of whole network. In the case of preferential tree extraction, for instance *Q. petraea* has a greater economical value than *Carpinus betulus,* therefore the more valuable tree is exposed to greater exploitation pressure. The mycorrhizal fungi community is relatively resilient and many species, the generalists can switch to different hosts, however, overexploitation by picking of mycorrhizal species linked to multiple tree hosts may cause major perturbation of the network.

To state a concluding remark, all mutualistic networks display comparable topologies, ectomycorrhizal fungi-woody host being included. Generally, when compared to antagonistic networks, these exhibit higher nestedness and lower modularity. For a particular group of mutualistic networks, those exhibiting a greater intimacy between partners, low connectance, high modularity and low nestedness are characteristic (Bascompte et al. 2003, Fontaine et al. 2011).

The presented bipartite mutualistic network shows particular traits such as: high species asymmetry, generalist nature of trees and several ectomycorrhizal fungi, the approximately equal amount of generalists and specialists among ectomycorrhizal partners combined with highly dissimilar traits compared to other mutualistic networks, high nestedness, high connectance and low modularity. This combination of network properties makes the ectomycorrhizal network singular among mutualistic bipartite networks due to the unique characteristic of the ectomycorrhizal fungi: they interconnect the trees.

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Appendix

Table 1 Presence-absence matrix of ectomycorrhizal community, Hoia forest, 1999-2011

Fungal species (v8 - v94)	v1- *Quercus cerris*	v2 - *Q. robur*	v3- *Q. petraea*	v4- *Tilia tomentosa*	v5- *Carpinus betulus* L	v6 - *Corylus avellana*	v7- *Q. pubescens*
v8 - *Coenococcum geophilum* Fr.	1	1	1	1	1	1	1
v9 - *Lactarius circellatus* (Battara) Fr.	1	1	1	1	1	1	1
v10 - *Amanita rubescens* (Pers. Fr.) Gray	1	1	1	1	1	1	1
v11 - *A. phalloides* (Vaill. ex Fr.) Link	0	0	1	1	1	0	0
v12 - *Leccinum duriusculum* (Schulzer ex Kalchbr.) Singer	0	0	0	0	1	0	0
v13 - *Russula foetens* (Pers.) Pers.	1	1	1	0	1	1	1
v14 - *R. cyanoxantha* (Schaeff.) Fr.	1	1	1	1	1	1	1
v15 - *Lactarius quietus* (Fr.) Fr.	0	0	1	0	1	1	0
v16 - *Russula fragilis* sensu Cooke	0	0	1	0	0	0	0
v17- *R. subfoetens* sensu Rea	0	0	0	0	1	0	0
v18 - *Lactarius vellereus* (Fr.) Fr.	0	1	1	1	1	0	1
v19 - *R. delica* Fr.	0	1	1	0	1	0	0
v20 - *Boletus chrysenteron* Bull.	1	1	1	1	1	0	1
v21 - *B. appendiculatus* Schaeff.	1	1	1	0	0	0	1
v22 - *B. porosporus* Imler ex. Watling	0	1	1	1	0	0	1
v23 - *R. velenovsky* Melzer & Zvara	0	0	0	0	1	0	0
v24 - *R. mairei* Singer	0	0	1	0	1	1	0
v25 - *R. consobrina* (Fr.) Fr.	0	0	1	0	1	0	0
v26 - *R. rosea* Pers.	0	0	0	0	1	0	0
v27 - *Boletus. aestivalis* (Paulet) Fr.	1	1	1	1	1	0	1
v28 - *B. queleti* Schulzer	0	0	1	1	0	0	0
v29 - *B. luridus* Sowerby	1	1	1	0	0	0	1
v30 - *Gyroporus castaneus* (Bull.) Quél.	0	0	1	0	0	0	0
v31 - *L. piperatus* (L.) Pers.	1	1	1	1	1	1	1
v32 - *L. volemus* (Fr.) Fr.	0	0	1	0	0	0	0
v33 - *Craterellus cornucopioides* (L. ex Fr.) Pers.	1	1	1	0	1	1	0
v34 - *Inocybe fastigiata* (Schaeff.) Quél.	1	1	1	1	1	0	0
v35 - *Scleroderma citrinum* Pers.	1	1	1	0	0	0	1
v36 - *R. cessans* Pers.	0	0	1	0	0	0	0
v37 - *B. subtomentosus* sensu Bolton.	0	0	1	0	0	0	0
v38 - *A. vaginata* sensu Stevenson	1	1	1	0	0	0	0
v39 - *R. virescens* (Schaeff.) Fr.	0	1	1	0	1	0	0
v40 - *Tricholoma saponaceum* (Fr.) P. Kumm.	0	1	1	0	0	0	1
v41 - *Leccinum carpini* (R.Schulz) M.M. Moser	0	0	0	0	1	0	0
v42 - *R. claroflava* Grove	0	1	1	0	0	0	0
v43 - *R. fellea* (Fr.) Fr.	0	1	0	0	0	0	0
v44 - *Hygrophorus eburneus* (Bull.) Fr.	0	0	1	0	0	0	0
v45 - *R. vesca* Fr.	0	1	1	0	1	0	0
v46 - *R. carpini* R. Girard & Heinem.	0	0	0	0	1	0	0
v47 - *A. citrina* sensu Stevenson	0	0	0	0	1	0	0

Table 1 (continuation)

Fungal species (v8 - v94)	v1- *Quercus cerris*	v2 - *Q. robur*	v3- *Q. petraea*	v4- *Tilia tomentosa*	v5- *Carpinus betulus* L	v6 - *Corylus avellana*	v7 - *Q. pubescens*
v48 - *Laccaria laccata* (Scop.) Cooke	1	1	1	1	1	1	1
v49 - *Laccaria amethystina* (Huds.) Cooke	0	1	1	1	1	0	0
v50 - *Hebeloma crustuliniforme* (Bull.) Quél.	1	1	1	1	1	0	1
v51 - *R. pectinatoides* Peck	0	0	1	0	1	0	0
v52 - *B. satanas* Lenz	1	1	0	0	0	0	1
v53 - *Cortinarius sp*.	0	0	1	0	0	0	0
v54 - *Amanta lividopallescens* (Secr. ex Boud.) Kühner & Romagn	0	0	1	0	0	0	0
v55 - *Amanita battarrae* (Boud.) Bon.	0	0	0	0	1	0	0
v56 - *Russula lepida* Fr.	0	0	1	0	0	0	0
v57 - *Russula aeruginea* Fr.	0	1	1	0	0	0	0
v58 - *Paxillus involutus* (Batsch) Fr.	0	1	1	0	1	1	0
v59 - *Inocybe rimosa* Britzelm	1	0	1	0	0	0	0
v60 - *Tricholoma virgatum* (Fr.) P. Kumm.	0	1	1	1	1	1	1
v61 - *Leccinum quercinum* Pilat	0	0	1	0	0	0	0
v62 - *R. nigricans* Fr.	1	1	1	1	1	0	0
v63 - *L. chrysorrhaeus* Fr.	0	0	1	0	0	0	0
v64 - *L. camphoratus* (Bull.) Fr.	0	0	1	0	0	0	0
v65 - *Amanita echinocephala* (Vittad.) Quél.	0	0	1	0	0	0	0
v66 - *R. romellii* Maire	1	0	1	0	0	0	0
v67 - *R. ionochlora* Romagn.	1	0	1	0	0	0	0
v68 - *R. atropurpurea* (Krombh.) Britzelm.	0	1	0	0	1	1	0
v69 - *Amanita virosa* (Fr.) Bertill.	0	1	1	1	1	0	0
v70 - *A. ceciliae* (Berk. & Broome) Bas.	0	0	1	0	0	0	0
v71 - *A. pantherina* (DC.) Krombh.	1	1	1	1	1	1	1
v72 - *L. fulvissimus* Romagn.	0	0	1	0	0	0	0
v73 - *R. brunneoviolacea* Crawshay	0	0	1	0	0	0	0
v74 - *R. alutacea* (Fr.) Fr.	0	0	0	0	1	0	0
v75 - *R. lepida* Fr.	0	0	0	0	1	0	0
v76 - *Scleroderma areolatum* Ehrenb.	0	1	1	0	0	0	0
v77 - *R. pelargonia* Niolle	0	0	0	0	1	0	0
v78 - *R. pseudointegra* Arnould & Goris	0	0	0	0	1	0	0
v79 - *Mutinus caninus* (Huds.) Fr.	0	0	0	0	1	0	0
v80 - *Phallus impudicus* L.	0	0	0	0	1	0	0
v81 - *Inocybe geophylla* (Fr.) P. Kumm.	0	0	0	1	1	0	0
v82 - *B. impolitus* Fr.	0	0	1	0	0	0	0
v83 - *R. heterophylla* (Fr.) Fr.	0	0	1	0	0	0	0
v84 - *Hydnum repandum* L.	1	1	1	0	1	0	0
v85 - *Ramaria stricta* (Pers.) Quél.	1	1	1	0	1	1	0
v86 - *L. blennius* (Fr.) Fr.	0	0	1	0	0	0	0
v87 - *R. aurea* Pers.	0	0	1	0	0	1	0
v88 - *B. pulverulentus* Opat.	0	0	1	0	0	0	0
v89 - *Russula decolorans* (Fr.) Fr.	0	0	1	0	0	0	0

Table 1 (continuation)

Fungal species (v8 - v94)	v1- *Quercus cerris*	v2 - *Q. robur*	v3- *Q. petraea*	v4- *Tilia tomentosa*	v5- *Carpinus betulus* L	v6 - *Corylus avellana*	v7- *Q. pubescens*
v90 - *L. scrobiculatus* (Scop.) Fr.	0	0	1	0	0	0	0
v91 - *Suillus granulatus* (L.) Roussel	0	1	1	1	0	0	0
v92 - *R. laurocerasi* Melzer	1	1	1	0	0	0	0
v93 - *B. edulis* Bull.	1	1	0	1	0	0	0
v94 - *Entoloma lividum* (Bull.) Quél.	1	1	1	1	1	1	0