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The macrofungal diversity and community of Atlantic oak *(Quercus petraea* and *Q. robur)* forests in Ireland

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Abstract

O'Hanlon, R. & Harrington, T.J. 2012. The macrofungal diversity and community of Atlantic oak *(Quercus petraea* and *Q. robur)* forests in Ireland. *Anales Jard. Bot. Madrid* 69(1): 107-117.

The oak species *Quercus petraea* and *Q. robur* are dominant canopy tree species of native deciduous forests in Ireland and coastal regions of Western Europe. These forests are typically plant species-rich, and can also have a rich fungal flora. This survey examined macrofungi found in five native oak sites across Ireland over three years. Overall, 94 macrofungal species belonging to 39 genera were discovered with *Mycena, Lactarius, Russula* and *Cortinarius* the most species-rich genera. The species accumulation curve did not show signs of levelling off, indicating that more sampling would reveal more new species. Species richness estimation using the Chao2 estimator indicated that up to 135 species may be present across all of our plots, with individual plots receiving estimates from 19 to 61 species per plot. Sampled-based rarefaction analysis showed no significant differences in macrofungal species richness between our plots. The five most common species were *Laccaria amethystina, L. laccata, Stereum hirsutum, Armillaria mellea* and *Cortinarius flexipes.* Comparisons of the results with results from oak forests in similar regions found that the communities in Great Britain were most similar to those found in Ireland. There were some key oak forest distinguishing fungal species from the family Boletaceae lacking from Irish oak forests. It is hypothesised that the historic deforestation of Ireland, caused a reduction of suitable habitats for Irish oak associated macrofungi, leading to the unspecific mycota found in the oak forests of this study. The threats to Atlantic oak forests in Ireland are briefly discussed.

Keywords: Fungi, ectomycorrhiza, functional groups, decomposer, biogeography.

Resumen

O'Hanlon, R. & Harrington, T.J. 2012. La comunidad macrofúngica y su diversidad en los bosques de roble *(Quercus petraea* y *Q. robur)* de Irlanda. *Anales Jard. Bot. Madrid* 69(1): 107-117 (en inglés).

Las especies de *Quercus petraea* y *Q. robur* se encuentran en bosques de Irlanda y regiones de influencia atlántica de Europa Occidental. Estos bosques, típicamente ricos en especies de plantas, presentan una abundante micobiota. Este estudio examina la diversidad de macromicetes en cinco bosques naturales de roble en Irlanda durante un periodo de tres años. En total se registraron 94 especies pertenecientes a 39 géneros, siendo *Mycena, Lactarius, Russula* y *Cortinarius* los de mayor presencia. La curva de acumulación de especies no mostró signos de nivelación, por lo que un mayor muestreo podría revelar la presencia de otras especies. La estimación de la riqueza de las especies usando Chao2 indicó que en el conjunto de las áreas estudiadas podrían aparecer hasta 135, con una media estimada de 19 a 61 especies por área. Un análisis de rarefacción no mostró diferencias significativas entre la riqueza de especies de macromicetes de las áreas estudiadas. Las especies más comunes fueron *Laccaria amethystina, L. laccata, Stereum hirsutum, Armillaria mellea* y *Cortinarius flexipes.* Nuestros resultados fueron muy similares a los de las comunidades del Reino Unido; sin embargo, algunos bosques de robles del Reino Unido presentaban especies de la familia Boletaceae ausentes en los bosques de robles irlandeses. Presentamos la hipótesis de que la histórica deforestación sufrida en Irlanda causó una reducción de los hábitat adecuados para los macromicetes asociados a los robles irlandeses, dando lugar a la micota inespecífica encontrada en los bosques de roble estudiados. También se realiza un breve comentario acerca de las amenazas a los bosques de roble en Irlanda.

Palabras clave: Fungi, ectomicorrizas, grupos funcionales, descomponedor, biogeografía.

INTRODUCTION

European white oak species (including *Quercus petraea* L. and *Q. robur* L.) survived the last glacial maximum period (18,000-20,000 years ago) in three isolated refugia: the Iberian, Italian and Balkan peninsulas, from which it subsequently spread northwards (Brewer & al., 2002) finally reaching Ireland and Britain at the beginning of the Holocene (Petit & al., 2002). The term "Atlantic oak woods" describes forests (i) with a canopy dominated by *Q. petraea* and *Q. robur,* (ii) situated along the Atlantic seaboard (Ireland, west coast of Wales, Scotland and England, and along the coast of mainland Europe from Northern Portugal to Norway, (iii) subject to a wet and humid climate, and (iv) with an abundance of lower plants (i.e. ferns, mosses and liverworts) (Baarda, 2005). Mature forests of Atlantic oak (*Q. petraea*) woods fall under the classification 'old sessile' oak woods with *Ilex* and *Blechnum* and are an annexed habitat according to EU Directive 92/43/EEC, thus indicating the need for conservation and management research in these habitats.

Oak reached Ireland about 9000 years ago (Mitchell, 2006), and spread throughout the country, forming dense forests, with elm, pine, ash and hazel being the other dominant canopy trees depending on soil types (Cross, 2006). The deforestation of Ireland's landscape started during the 13th century, as land was cleared for agricultural crops and grazing for livestock. Further declines in tree species, particularly *Quercus* and *Betula,* occurred during the 18th century as the wood was needed to fuel iron-smelting industries (Cole & Mitchell, 2003). Anthropogenic influence

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Table 1. Descriptions of the five oak forests surveyed in this study. The ectomycorrhizal (except ash) tree species present inside the plots are also listed. Soil description was taken from the geological maps of Ireland (Gardener & Radford, 1980). Vegetation classification follows the Irish habitat classification system (Fossitt, 2000). Data for ectomycorrhizal tree species, site age and pH are taken from O'Hanlon (2011).

Site	Ectomycorrhizal Tree species present	Minimum age	pH	Vegetation classification	Principle soil	Parent material
Raheen	Qp, Ca, Fs	140	4.83	WN1	Grey brown podzol	Limestone glacial till
Tomies	Qp, Bp,	210	5.56	WN1	Brown podzol	Sandstone
Abbeyleix	Qr, Bp, Fs, Ld,	200	5.67	WN2	Grey brown podzol	Stony Limestone glacial till
Union	Qp, Ca, Fs	200	7.11	WN1	Grey brown podzol	Limestone glacial till
Kilmacrea	Qp, Ca	160	5.01	WN1	Acid brown earths	Ordovician-Cambrian shale

Abbreviations: Qp, *Quercus petraea* L.; Ca, *Corylus avellana* L.; Fs, *Fagus sylvatica* L.; Bp, *Betula pubescens* Ehrh.; Qr, *Quercus robur* L.; Ld, *Larix decidua* Mill.; WN1, oak-birch-holly woodland; WN2, oak-ash-hazel woodland.

over the centuries has reduced the area of native woodland in Ireland to less than 1% of the land area, one of the lowest levels in Europe (Forest Resources Assessment, 2010). Oak forests currently cover 14,600 ha of Ireland's area or almost 2.5% of the forest cover (National Forest Inventory, 2007), although this value includes plantation oak forests. Oak reached Britain at roughly the same time as it arrived in Ireland; with forests currently covering 222,697 ha of Britain, or over 9% of the forested area (National Forest Inventory, 2003). Atlantic oak forests are also the climax vegetation type in the North-west of Spain and are thought to have established as early as 12,000 years BP (Brewer & al., 2002). *Quercus robur/Q. petraea* cover 298,000 ha, or over 1% of the forested area in Spain (Anonymous, 2007). In the region of Galicia, *Q. robur* is estimated to cover 187,789 ha or 14% of the total wooded area of the region (Anonymous, 2001), while also being a dominant forest climax tree in the Northern – most parts of the region of Cantabria (Guinea, 1954).

Quercus is an ectomycorrhizal (ECM) host, with over 230 ECM fungi known to associate with it in Britain (Newton & Haigh, 1998), and many saprotrophic and parasitic fungi are found in *Quercus* forests in Western Europe (Wilkins & al., 1937; Hering, 1966; Watling, 1974, 2005a). To date, there has been no systematic study of the macrofungal diversity of Irish oak forests. Indeed, Ireland's forests have received little by way of systematic mycological surveys (O'Hanlon & Harrington, 2011a). Of the two available published records for macrofungi from Irish oak forests, one comes from a British Mycological Society visit to the Atlantic oak woods of the Killarney valley (Ramsbottom, 1936) and the other is from the first catalogue of Irish fungi (Muskett & Malone, 1978, 1980). In contrast, the oak forests of Britain have received much more detailed and systematic studies (Wilkins & al., 1937; Hering, 1966; Watling, 1974, 2005a; Humphrey & al., 2003). Other macrofungal studies of Atlantic oak woods have been carried out in Northern Spain (Losa España, 1946; Losa Quintana, 1974; Sarrionandia & al., 2009) and France (Buee & al., 2011). Watling (2005a) compares the macrofungal diversity of Scottish, English and mainland European oak forests, and concludes that the mycota of Scottish oak woods is an impoverished version of that of English oak woods, which in turn is an impoverished version of that found in mainland European oak woods. It is not known where Irish oak woods fit into this sequence. In its migration after the Holocene, oak most likely brought many of its current symbiotic ECM partners with it northward into Ireland and Britain from mainland Europe. As oak is said to have entered Britain and Ireland from a common source, utilizing land-bridges present at the time (Mitchell, 2006), it might be expected that their macrofungal communities would share many commonalities with that of European Atlantic oak forests. Co-migration of host and symbiont has already been identified in many studies examining ECM biogeography in North and South America (Halling, 2001; Halling & al., 2008).

This research was part of a larger project (FUNCTIONALBIO project, Bolger & al., 2009) investigating the diversity of soil decomposers and predatory and parasitic arthropods in Irish forests. The results for the macrofungal communities of the non-native Sitka spruce *Picea sitchensis* (Bong.) Carr. forest type; the below-ground and above-ground ECM communities of these forests; and for the differences in macrofungal communities between the forest types have been published elsewhere (O'Hanlon & Harrington, 2011b; 2012a; 2012b). Only the macrofungal results from the oak forest plots will be dealt with in this article. The objectives of this article are to describe the macrofungal communities of Atlantic oak (*Q. petraea* and *Q. robur*) forests in Ireland. It is expected that the macrofungal communities of Irish Atlantic oak forests would be similar to that found in Atlantic oak forests in Britain and mainland Europe, due to the common source of origin and the similar climatic conditions experienced in these habitats.

MATERIAL AND METHODS

Site selection

The sites were selected from a list of previously surveyed sites during the BIOFOREST project (Iremonger & al., 2007) and from sites known to be mature oak forests. Five mature (>100 years) oak woods were visited at least 3 times over the period 2007 to 2009 inclusive (Table 1; Fig. 1). Due to sampling restrictions, only Kilmacrea and Raheen were visited in all three years. The remaining sites were visited in 2008 and 2009. In each site, a 100 m^2 permanent plot was established in an area that was considered typical of the site (similar aged trees, similar vegetation type, level topography, large distance to forest edge). The overall project (O'Hanlon, 2011) investigated 27 forest plots from a selection of four forest types (oak, ash *Fraxinus excelsior* L.,

Scots pine *Pinus sylvestris* L. and Sitka spruce) across 12 counties in Ireland, and compared the macrofungal aspect of the forest types according to species richness and community structure. Thus, due to time restrictions and sampling implications related to even sampling across sites, our sampling had to be restricted to one plot per site. Four of the sites (Raheen, Tomies, Kilmacrea, Union) fitted the WN1 grouping for woodlands from the Irish habitat classification system and the remaining site (Abbeyleix) fitted the WN2 grouping (Fossitt, 2000). The WN1 is the grouping for the oak-birch-holly woodland, consisting of a canopy dominated by *Q. petraea* and with a ground flora dominated by Ling (*Calluna vulgaris* (L.) Hull.), Bilberry (*Vaccinium myrtillus* L.), Bracken (*Pteridium aquilinum* (L.) Kuhn.), Hard Fern (*Blechnum spicant* (L.) Sm.), Great Wood-rush (*Luzula sylvatica* (Huds.) Gaudin.), Velvet Bent (*Agrostis canina* L.), Common Cow-wheat (*Melampyrum pratense* L.), Wood Sage (*Teucrium scorodonia* L.) and Honeysuckle (*Lonicera periclymenum* L.). The WN2 grouping describes the oak-ash-hazel woodland grouping, consisting of a canopy dominated by *Q. robur* and a ground flora dominated by Ivy (*Hedera helix* L.), Wood Anemone (*Anemone nemorosa* L.), Bluebell (*Hyacinthoides non-scripta* (L.) Chouard ex Rothm.), Wood Speedwell (*Veronica Montana* L.), Barren Strawberry (*Potentilla sterilis* (L.) Garcke.) and the ferns *Dryopteris filix-mas* (L.) Schott., *Polystichum setiferum* (Forssk.) Woynarand and *Athyrium filix-femina* (L.) Roth. The major difference thought to be the deciding factor as to whether *Q. petraea* or *Q. robur* dominate a site is the soil nutrient and drainage status, with *Q. robur* becoming dominant on calcarious well drained soils (Cross, 2006).

All of the chosen sites are exposed to similar levels of rainfall and temperature, and consequently have similar soil moisture content (O'Hanlon, 2011), due to the temperate maritime climate of Ireland.

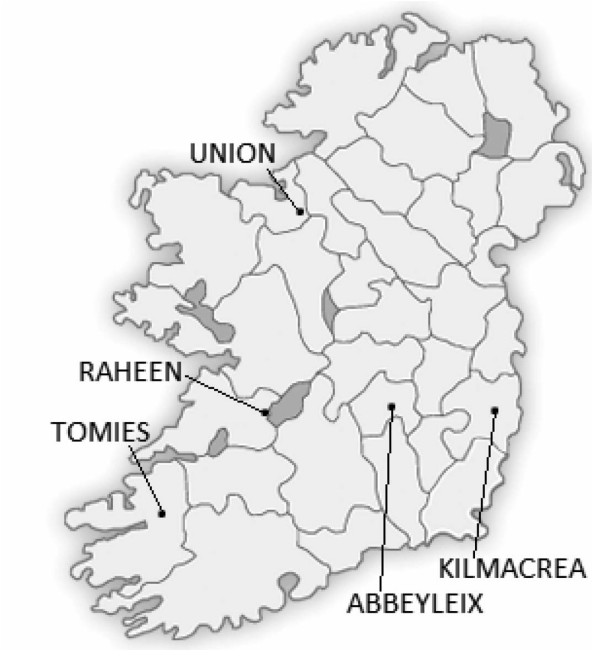

Fig. 1. Map of Ireland indicating the sites surveyed.

Macrofungal assessment

The plots were visited at least twice in the autumn (August-November) of 2007, 2008 and 2009. All macrofungal sporocarps (mushrooms) inside the plots were identified *in situ* where possible, and sporocarps of unidentified species were retained for later identification according to a standard approach (Courtecuisse & Duhem, 1995). Following the definition of macrofungi from Watling (1995), we collected and identified all fungi which were visible to the naked eye and generally produced sporocarps greater than 5 mm in diameter. The full list of macrofungal species and their respective authorities included in this paper are given in Appendix 1. The macrofungal species recorded were split into functional groups based on their primary mode of nutrition; litter decay (LD), ectomycorrhizal (ECM), parasitic (P) and wood decay (WD) groups (Ferris & al., 2000). We examined functional group diversity as well as species diversity, because it can highlight differences in the macrofungal communities of different forest types, and has been used in the past as a framework to describe the macrofungal community of British oak woods (Watling, 1974).

We examined the species richness and functional group richness of fungi in the oak forests. Species richness is the total number of species found. Functional group richness is the number of species found which fit into one of the predefined functional groups i.e. LD, ECM, P and WD. The number of plots in which a species was recorded over the three years was used to give an indication of the distribution level of that species in oak forests throughout the Republic of Ireland. The number of sporocarps recorded over the three years in the plots was used as a measure of species abundance.

Statistical analysis

To compare the species richness of the different plots and forest types at a similar sampling intensity, sample-based rarefaction curves with 95% confidence intervals were calculated, using the computer program EstimateS version 8.2 (Colwell, 2004). In these analyses, plots were sampled randomly with re-placement, over 500 permutations of the data, because otherwise confidence intervals are meaningless in the upper end of the rarefaction curve (Colwell & al., 2004). The data used for the rarefaction and species richness estimation consisted of the presence/absence matrix of the species in each plot visit. Rarefaction curves read from right to left and are used for estimating species richness at a standard, smaller sample size. In order to statistically estimate the total species richness in the forest plots, species richness estimation was carried out using EstimateS version 8.2. The Chao2 diversity estimator was calculated for the plots, as this has been identified as an estimator which is suitable for fungal data (Unterseher & al., 2008). This richness estimator is an incidence based estimator that uses the ratio of species found in only one sample (plot visit) to species found in two or more samples. It has

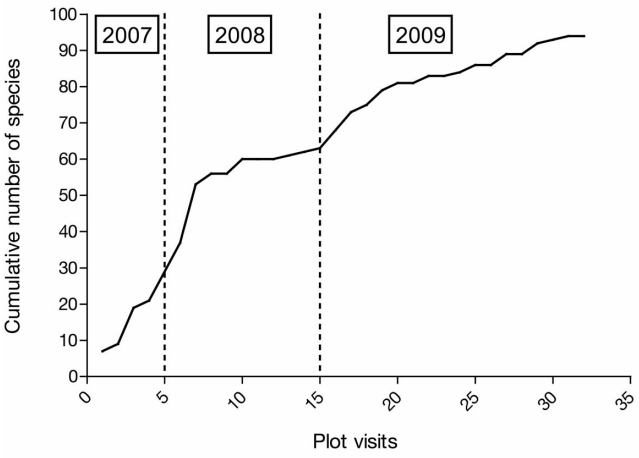

Fig. 2. Cumulative number of macrofungal species recorded over the duration of the study. The years of the study are separated by vertical dashed lines.

the benefit of using incidence data only, as abundance based estimators have been shown to be negatively affected by populations which are non-randomly (patchy) distributed (Longino & al., 2002). Fungal populations have been shown to be non-randomly distributed in nature (Taylor, 2002) and so abundance based estimators may fail to return likely estimates.

RESULTS

A total of 94 macrofungal species belonging to 39 genera were identified from Irish oak forests (Appendix 1). After three years and 31 plot visits new species were still being discovered on a regular basis (Fig. 2). Using the Chao2 species richness estimator, a total of up to 135 species are estimated to be found across the five plots, indicating that we recorded some 70% of the total species richness of our oak plots using our sampling scheme and survey duration. The recorded species consisted of 39 ECM (42%), 33 LD (35%), 20 WD (21%) and 2 P (2%) species (Fig. 3). The most species rich genera were *Mycena* (15), *Lactarius* (8), *Russula* (8) and *Cortinarius* (7) with no other genus having more than 4 species. Despite the high species richness of macrofungi collected from the plots, over 55% of the species were found only once (Fig. 4). The most common species (based on presence out of the five plots) were *Laccaria amethystina, Laccaria laccata, Stereum hirsutum, Armillaria mellea, Cortinarius flexipes, Marasmius hudsonii, Mycena galopus, Russula ochroleuca, Xylaria hypoxylon* and *Crepidotus variabilis*. The first three species were present in all five plots, the following six species were present in four of the plots, while the final species, *C. variabilis*, was present in three plots (Table 2). The plot at Abbeyleix was the most species-rich, while the plot at Union had the lowest species richness, although not significantly lower (P>0.05) based on comparisons at a similar sampling intensity using sample-based rarefaction estimates (Fig. 5). According to the Chao2 species richness estimates, Kilmacrea is possibly the most species rich plot (61 species), with Union showing the lowest species richness estimates (19 species) (Fig. 5). The mean number of species recorded from each plot visit was 7.7 species with a maximum of 18 species (Raheen) recorded on a single plot visit.

Functional group richness patterns

Of the 39 species in the ECM functional group, the ten most common macrofungi (based on distribution out of the five plots) are *Laccaria amethystina, Laccaria laccata, Cortinariuns flexipes, Russula ochroleuca, Cortinarius acutus* and *Lactarius quietus* being found in five, five, four, four, three and three plots respectively. Of the 33 LD species found, the most widely-distributed were *Mycena hudsonii, Mycena galopus, Lycoperdon nigrescens, Lycoperdon perlatum, Marasmiellus ramealis, Marasmius androsaceus* and *Mycena leptocephala*, the first two species being found in four plots with the remaining species being found in three plots. Within the WD functional grouping, *Stereum hirsutum, Xylaria hypoxylon* and *Crepidotus variabilis* were found in five, four and three plots respectively. Parasitic species were rare overall, with only *Armillaria mellea* being present in four plots.

Sporocarp abundance patterns

In general the species which were most common based on occurence out of the five plots (Table 2) were the same as the species which produced the most sporocarps over the course of the study. However, certain species were more locally common and abundant in some plots based on abundance of sporocarps. *Scleroderma citrinum, Lycoperdon nigrescens, Lycoperdon perlatum*, and *Lactarius quietus* were all abundant in the plots in which they were found with 93, 39, 38 and 31 sporocarps respectively. *Scleroderma citrinum* in particular stands out as a more locally common species, as it was found to have the third highest sporocarp abundance (93 sporocarps), but only found in two sites (Abbeyleix and Kilmacrea). It was extremely abundant in the Abbeyleix site, with double the abundance of the next most abundant species there (*Laccaria laccata*, 44 sporocarps). In the Kilmacrea plot, the parasitic species *Armillaria mellea* was much more abundant (34 sporocarps) than in the rest of the plots. The Raheen plot had a large abundance of *Ly-*

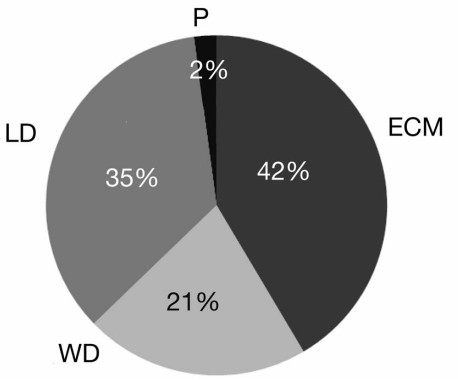

Fig. 3. Functional group breakdown of the macrofungal species ($n = 94$) found in the plots. LD, litter decay; ECM, ectomycorrhizal; P, parasitic; and WD, wood decay species.

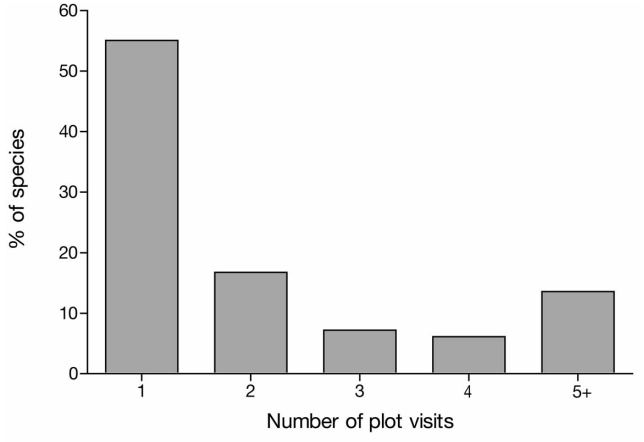

Fig. 4. Sampling effort based on the number of occasions on which a species was found.

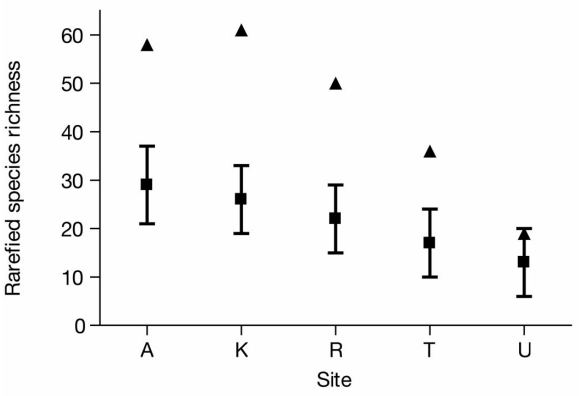

Fig. 5. Estimates of species richness of the sites based on rarefaction (square symbols with upper and lower 95% confidence limits) and Chao2 species richness estimation (triangle symbols). Rarefaction was carried out at the standard sampling intensity of four plot visits. Both sample-based rarefaction and Chao2 estimates were generated using 500 randomized samples with replacement from the plot based sample results. Site abbreviations: A, Abbeyleix; K, Kilmacrea; R, Raheen; T, Tomies; U, Union.

coperdon perlatum and *L. nigrescens*, while these species were not abundant in the rest of the plots.

Two of the species found are prized for their edibility in many countries, these are the bay bolete *Boletus badius* and the chanterelle *Cantharellus cibarius*. However, the abundances of these species were very low in the plots. Incidentially, although not found within our plot and therefore not included in the species list (Appendix 1), the autumn chanterelle *Cantharellus tubaeformis* (Bull.) Fr. was found outside of the Tomies plot and also in large quantities.

DISCUSSION

Species and functional group richness of Atlantic oak forests

Over three years, the total species richness found in Irish Atlantic oak forests was similar to that found in comparable Spanish (Sarrionandia & al., 2009) and French (Buee & al., 2011) oak forests yet much lower than that found in oak forests in the Britain (Humphrey & al., 2003) at 94 versus 78, 84 and 284 species respectively. However, the Humphrey & al. (2003) study examined 6400 m^2 of oak forest, compared to the 500 m^2, 800 m^2 and 2000 m^2 examined in this study and the Sarrionandia & al. (2009) and Buee & al. (2011) studies respectively. Previous work by Losa Quintana (1974) in the Northern part of the provinces of Lugo and La Coruña identified 72 macrofungal species from *Q. robur* forests from a single plot visit to 1200 m^2 of oak forest. A longer and more extensive study (over five years and including entire forests) of British oak forests by Wilkins & al. (1937) recorded 391 macrofungal species in twenty *Q. robur* forests. One of the few studies to examine *Q. petraea* forests in Britain, Hering (1966) found 88 species from sampling 300 m^2 of oak forest over three years. It is evident from the previous discourse that direct comparisons between the macrofungal species richness of the aforementioned studies cannot be carried out due to differences in actual physical area sampled and in the duration and frequency of plot visits between the studies. Attempting to equate the listed studies on a similar sample basis is difficult, as mean species per m^2 sampled, takes no account of the change in fungal community over different sample years, and mean species per plot visit takes no account of the total area sampled. Forest macrofungal abundances and communities are known to vary widely from year to year (Straatsma & al., 2001; Krebs & al., 2008), and the numbers of macrofungal species has been shown to be positively related to area surveyed (Peay & al., 2007). Comparisons between the listed studies are also difficult as soil chemistry (Ruhling & Tyler, 1990), vegetation community (Villeneuve & al., 1989; Gabel & Gabel, 2007), forest age (Kranabetter & al., 2005) and forest tree species (Buee & al., 2011) have been shown to have an effect on the macrofungal communities of forests.

A caveat of our study was our restricted sampling scheme, which focussed on a single 100 m^2 plot per site. This size restriction was necessary due to the overall design of the project, which sought to relate micro-arthropod and macrofungal diversity between many forest types composed of geographically distant forest sites. However, the effect of the restricted sampling may not have been too adverse to our description of the macrofungal community of these forests, as we found that extending our survey area to roughly 1000 m^2 across all plots studied (including ash, oak, Scots pine and Sitka spruce sites) only increased our total species richness by a further 17% (R. O'Hanlon, unpublished data). Moreover, macrofungal sampling of Scots pine and Norway spruce forests in England has found that 100 m^2 plots can record up to 80% of the species richness of a homogenous forest area. That said, macrofungi are known to have patchy distributions across forest environments, related to ECM host specificity (Ishida & al., 2007), substrate preferences (Tedersoo & al., 2008) and soil abiotic conditions (Rühling & Tyler 1990), therefore a larger plot which encapsulates more of these micro-sites would include more macrofungal diversity. The use of sporocarps as a definitive

Table 2. Frequency data for the ten most distributed macrofungal species. Data shows the number of plot visits on which the species was present. The total number of plot visits to a site is given (in parenthesis) after the site name.

Species or functional group	Abbeyleix (5)	Kilmacrea (7)	Raheen (9)	Tomies (6)	Union (4)
Laccaria amethystina	4	1	2	5	3
Laccaria laccata	5	3	1	3	3
Stereum hirsutum	4	3	4	3	3
Armillaria mellea	1	3	1	0	2
Cortinarius flexipes	0	4	3	2	1
Marasmius hudsonii	1	1	2	1	0
Mycena galopus	1	2	1	0	2
Russula ochroleuca	1	2	1	4	0
Xylaria hypoxylon	2	1	0	1	1
Crepidotus variabilis	0	2	1	0	1
Litter decay species richness	14	12	18	6	5
Ectomycorrhizal species richness	12	16	20	14	3
Parasitic species richness	2	1	1	0	1
Wood decay species richness	6	6	10	6	6
Total species richness	34	35	49	26	15

indicator of species presence has been found to be somewhat unreliable (Dahlberg & al., 1997; Durall & al., 2006). However, in the absence of costly Next Generation environmental sequencing technologies, it is still a relevant and useful method of examining fungal ecology in the field (Toth & Barta, 2010). Associated work relating the below-ground (ECM roots) to the above-ground (ECM sporocarp) communities of these oak plots found large differences between the taxa richness and ECM communities of both systems (O'Hanlon & Harrington, 2012a). While actual differences do exist in these above- and below-ground communities related to such factors as non- epigeous sporocarp producing ECM fungi and species that produce minute sporocarps; differences in sampling intensity between the two systems no doubt added to these above- and below-ground disparities. Indeed, very few of the species found to be frequent below-ground were found as sporocarps. Conversely though, all except one (*Paxillus involutus*) of the epigeous sporocarp producing species found below-ground were found as sporocarps during this study, namely *Amanita citrina, Laccaria laccata, Laccaria amethystina, Russula nobilis, Russula ochroleuca* and *Scleroderma citrinum*.

When comparing the differences in functional groups, the use of percentages lessens the effect of different sampling methodology between the listed studies. In agreement with the ECM proportion of the species found in this study, previous work in oak forests has found between 40 and 60% of the species found to be ECM (Losa Quintana, 1974; Humphrey & al., 2003; Sarrionandia & al., 2009); a finding common from many different forest types worldwide (Watling, 1995). The proportion of WD species varies between studies, this study found 21% WD fungi while work in Britain (Humphrey & al., 2003), North western Spain (Losa Quintana, 1974) and in the Basque region (Sarrionandia & al., 2009) have found 20, 18 and 14% WD species respectively. The differing species richness levels of WD fungi may be related to many forest variables. One factor which has a large effect on the fruiting of WD fungi is the moisture content of the substrate (Boddy, 1999). Varying levels of precipitation between the Irish, British and Spanish regions may have an effect on the WD species capable of colonising the oak wood; or physical factors such as the availability of woody debris may have an effect on WD species richness. Volumes of woody debris were positively related to the species richness of WD fungi in British coniferous forests (Ferris & al., 2000).

Macrofungal communities of Atlantic oak forests

This study of Irish oak woods has shown that they are particularly species-rich in the genera *Mycena*, *Lactarius*, *Cortinarius* and *Russula*; a finding similar to that of other macrofungal studies in Atlantic oak forests (Fig. 6). However, these genera are also some of the most species-rich genera worldwide (Kirk & al., 2008), with the genera *Cortinarius*, *Russula*, *Mycena* and *Lactarius* being the first, fourth, sixth and eight most species-rich genera of macrofungi recorded in Britain, Ireland and Northern Ireland (O'Hanlon & Harrington 2011a); so their high species richness may not be a distinguishing factor of Atlantic oak forests. Between the plots, there were some notable anomalies in macrofungal communities. Species such as *Marasmius hudsonii, Marasmius androsaceus*, and *Crepidotus variabilis* were present in moderate to large frequencies in some plots while being totally lacking from others. The first species is found on holly *Ilex aquifolium* L. leaf litter, and the absence of holly at the Union is the most likely reason for its absence. Evergreen plants and shrubs such as holly and ivy *Hedera helix* are common understory components of Irish oak woods (Kelly, 2005). *Marasmius androsaceus* was found growing on decaying bramble *Rubus fructicosus,* and lack of bramble in the Tomies and Union sites was the most likely reason for its absence in these two plots. The species *Crepidotus variabilis* was absent from the plots at Abbeyleix and Tomies, but it was found in the vicinity of the plot at Tomies. *Crepidotus variabilis* was found on wood and litter of *Q. robur* in Sweden (Tyler, 1992), therefore its absence from the Abbeyleix plot may be due to the local rarity of this species.

Watling (2005a) describes the macrofungal community of Atlantic oak forests in Scotland, highlighting 57 species

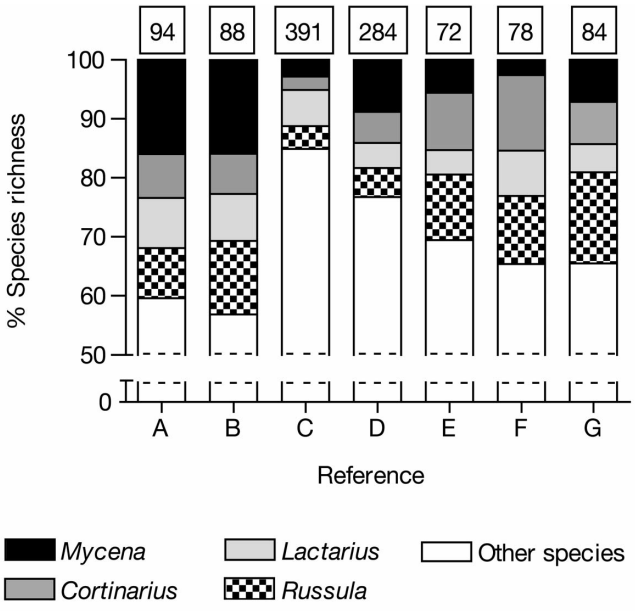

Fig. 6. Species rich genera of macrofungi found in previous studies of Atlantic oak forests. Figures in text box are total species richness found in *Quercus* forests from the studies. Note break in Y-axis at Y = 5-50. Study references: A, This study; B, Hering, 1966; C, Wilkins & al., 1937; D, Humphrey & al., 2003; E, Losa Quintana, 1974; F, Sarrionandia & al., 2009; G, Buee & al., 2011.

shown to be indicative of, or commonly found in, Scottish Atlantic oak forests. Of these species only *Armillaria mellea, Fistulina hepatica, Lactarius quietus, Russula nobilis, Russula ochroleuca, Scleroderma citrinum, Stereum hirsutum* and *Trametes versicolor* were found with oak in this survey; all except *Russula ochroleuca* showing some fidelity to the oak forest type in a related study (O'Hanlon, 2011). Both of the latter two species were found as sporocarps with oak, but also with other tree species in a study in France (Buee & al., 2011), indicating that they may not be specific to oak forests. Research by Watling (1974) identified a group of macrofungi from the family Boletaceae, specifically from the genera *Leccinum* and *Boletus* as typifying British oak woods. In the Irish oak woods of this study-members of the family Boletaceae were found to be very rare; indeed the entire clade Boletales is species-poor in Ireland and Northern Ireland when compared to the levels seen in Britain (O'Hanlon & Harrington, 2011a). Watling (1974) also identified fifteen species from the family Russulaceae, of which only one (*Lactarius quietus*) was found in the oak woods in this survey. One of the two species of *Boletus* found in this study was *Boletus badius*, a common ECM species not generally thought to associate with oak. This species was most likely present in association with birch (*Betula alba* L.) in the Tomies site and the hazel (*Corylus avellana* L.) in the Kilmacrea site. Three other species which are often regarded as common oak forest fungi are *Gymnopilus quercophilus* (Pouzar) Antonín & Noordel., *Stereum gausapatum* (Fr.) Fr., and *Peniophora quercina* (Pers.) Cooke. The first of the previously mentioned species was found to be very rare in the recent British study of fungi in oak forests (C. Quine, unpublished data), being found only in the very old (>170 years) oak woods at Alice Holt forest, while in the same study *Stereum gausapatum* was found to be widely distributed across oak forests of different ages. While the absence of *Stereum gausapatum* and *Peniophora quercina* from our plots is likely due to overlooking, these species are common in Northern Ireland (FRDBI, 2009), our results and the results from Britain (Humphrey & al., 2003; Watling, 2005a) and elsewhere across Europe (Galán & al., 1983; Lisiewska, 1994) indicate that *Gymnopilus quercophilus* may be rare in oak forests across Europe.

Comparison of the Irish Atlantic oak macrofungal community with that of their British counterparts (Humphrey & al., 2003; C. Quine, unpublished data) reveals many similarities between the two macrofungal communities. The species *Mycena galopus, Mycena leptocephala, Stereum hirsutum, Russula ochroleuca, Lactarius quietus, Laccaria amethystina, Laccaria laccata*, and *Crepidotus variabilis* show similarly high distribution levels in the Atlantic oak forests of both regions. Although from our data and the British data (C. Quine, unpublished data) only *Stereum hirsutum, Lactarius quietus* and *Crepidotus variabilis* show any fidelity to the oak forest type. Overall, there are few disparities between these two regions, although *Mycena sanguinolenta* and *Collybia dryophila* are slightly more common in British Atlantic oak forests. An interesting similarity with Britain (Humphrey & al., 2003; C. Quine, unpublished data) is the number of species from oak forests which seem to grow just as prolifically in Sitka spruce plantations. The phenomenon known as "host shifting" (Watling, 1995) may be occurring in Irish and British plantation Sitka spruce forests, whereby species normally common in native forests are abundant in forests of the exotic species. Examples of these species which are of similar abundance in our oak plots and also in Irish Sitka spruce forests (O'Hanlon and Harrington, 2011b) were *Clavulina coralloides, Laccaria amethystina, Lactarius tabidus* and *Leotia lubrica*, of which none are found with Sitka spruce in its home range (Outerbridge, 2002).

Comparisons of the macrofungal communities of Irish and Spanish Atlantic oak forests (Losa Quintana, 1974) reveals noticeable similarities in the distributions of some species, with *Laccaria laccata, Lactarius quietus, Lycoperdon perlatum, Mycena galopus* (listed as *Mycena galopoda*) and *Xylaria hypoxylon* being common in Atlantic oak forests in both regions. However, there are also distinct differences between the two communities, for example some species are much more common in Irish oak forests (e.g. *Cortinarius acutus, Cortinarius flexipes, Marasmius hudsonii*) while others are more common in Spanish counterpart forests (e.g. *Amanita citrina, Cantharellus cibarius, Mycena epipterygia*). Larger discrepancies are found between the macrofungal communities of Atlantic oak forests in Ireland and the Altube region of Northern Spain (Sarrionandia & al., 2009). These communities share few similarities regarding species common in both regions; with just *Laccaria amethystina* and *Lycoperdon perlatum* being of similar distribution. Moreover, marked differences in the distributions of

many species between the two regions exist, with many species being more common in Irish (e.g. *Lactarius quietus, Russula ochroleuca, Stereum hirsutum, Armillaria mellea, Mycena galopus* and *Cortinarius flexipes*) or Spanish oak forests (*Amanita citrina, Cortinarius cinnamomeus* (L.) Fr., *Craterellus cornucopioides* (L.) Pers., *Tricholoma sulphureum* (Bull.) P. Kumm. and *Lactarius chrysorreus* (Fr.). Surveying of French Atlantic oak forests (Buee & al., 2011) found species distributions broadly similar to those found in Irish oak forests, with the species *Lactarius quietus*, *Laccaria laccata, Laccaria amethystina*, *Mycena galopus* and *Stereum hirsutum* being widely distributed in oak forests of both regions.

Lack of specific macrofungal communities in Atlantic oak forests

Watling (1974, 2005a) found it difficult to clearly define characteristic macrofungal communities of Atlantic oak forests in Britain. It is evident from the above discussion that the oak communities of Irish Atlantic oak forests are also difficult to clearly delimit; and therefore we agree with previous research which states that the macrofungal community of oak forests contains few clearly distinctive elements (Tyler, 1992; Wilkins & al., 1937; Watling, 1974, 2005a). One species that can unanimously be described as typical of Atlantic oak forests, and oak forests in general is *Lactarius quietus*; being found with oak species across Europe (Heilmann-Clausen & al., 1998). Other species such as *Laccaria laccata, Laccaria amethystina, Stereum hirsutum* and *Xylaria hypoxylon* are all common in oak forests in Ireland, Britain, Northern Spain and France; however they are also common with many other deciduous and coniferous trees (Legon & Henrici, 2005). In the past, distinctive macrofungal communities have been described in forests dominated by alder (*Alnus* spp.) (Brunner & al., 1992), beech (*Fagus sylvatica*) (Tyler, 1992), birch (*Betula* spp.) (Watling, 1984; Orton, 1986), Scots pine (*Pinus sylvestris*) (Orton, 1986), spruce (*Picea rubens*) (Bills & al., 1986) and willow (*Salix* spp.) (Watling, 1992).

There may be numerous factors causing the formation of distinctive communities in the previously mentioned ecosystems, with ECM host specificity and soil abiotic conditions being noted as two of the strongest controlling factors driving macrofungal community assemblages in forests (Dahlberg, 2001). Many ECM fungi have been noted as showing high levels of host tree specificity, although the majority of fungal genera and species show only moderate to low specificity patterns (Molina & al., 1992). In Britain, the genus *Quercus* has been noted as having 233 ECM fungi associated with it from sporocarp studies, although only 13% of these species are restricted to *Quercus*. Both *Betula* and *Fagus* have more host specific fungal species in Britain, both showing high specificity for 18% of their known ECM associates (Newton & Haigh, 1998). In France, oak and beech forests are known to share many common macrofungi, 64% of species richness found in oak was also found in beech forests (Buee & al., 2011). This pattern of community similarity between oak and beech forests is also found in Scotland, Watling (2005a) conjectures that it may be due to the later arrival of beech into Britain, bringing with it its own fungal community, a community which went on to oust some of the oak-specific macrofungi from oak woods and lead to their reduction in distribution or extinction from the Scottish oak woods. If this is true, then a similar occurrence may have happened in Ireland, reducing the specificity of the oak macrofungal community as in the Scottish example. However, the lack of specific macrofungal communities in Irish oak forests was no doubt amplified by the historic removal of Ireland's native oak forests. Oak forests are the likely climax vegetation for the majority of Ireland (Cross, 2006), but anthropogenic influence since the 14th century has reduced the area of native oak woodlands to the remaining scattered patches across Ireland (Cole & Mitchell, 2003). This removal of the oak forests would have reduced the available habitats for many oak-specific ECM and decay fungi, as ECM fungi cannot survive in the absence of a host supply of carbohydrate (Högberg & al., 2001). This would explain the low species richness of oak specific ECM macrofungi (i.e. from the family Boletaceae) and indeed the low species richness of ECM fungi in general found in Ireland, although lack of macrofungal surveys is also a contributory factor (O'Hanlon & Harrington, 2011a).

Atlantic oak woods have been recognised as having high biodiversity in a range of organism groups, including vascular plants, bryophytes, lichens, invertebrates, birds and fungi (Malcolm & al., 2005). O'Hanlon and Harrington (2011a) identified the Atlantic oak woods of Ireland as habitats that likely had high macrofungal diversity, and also put forward preliminary guidelines to promote macrofungal conservation in Ireland. In agreement with Watling (2005b), they noted that the most effective way to conserve macrofungi is to preserve the habitat in which they are found. At present, the main threats to Irish and British Atlantic oak woods are the (i) lack of natural regeneration due to deer (*Cervus Nippon* Temminck) browsing, (ii) invasion of non-native plants such as *Rhododendron ponticum* L. and, (iii) replacement of forests with non-native species plantations (Jones, 2006). In all three of the above points, the removal of the oak component of the forest would have large effects on the diversity and community of macrofungi of the forest. Previously, the results of a long term study investigating the use of fencing to increase natural regeneration in Ireland's oak forests indicated that oak seedling survival was higher in areas where large browsing ungulates were absent (Kelly, 2002), although a complete lack of grazing has recently been found to be unfavourable to long-term woodland plant diversity (Perrin & al., 2011). The invasion of Rhododendron has a twofold negative effect on oak regeneration, firstly by shading out young oak seedlings and secondly by providing ample shelter for the deer, thus increasing oak browsing by deer (Cross, 1981). Regarding the third threat to Atlantic oak woodlands listed above, although the levels of oak planting have increased in the recent past in Ireland (National Forest Inventory, 2007). Currently, planting of native species including oak, is encouraged in Ireland by the provision increased grants for using

native species in forest planting. It is through effective conservation of our existing scattered oak forests and continued promotion of oak forest plantings that the conservation of Atlantic oak associated macrofungi can be carried out.

In conclusion, we found that the macrofungal assemblage of Irish Atlantic oak forests is very species-rich, with its community made up of many generalist species. Low similarity between mature oak forests in Ireland, Britain and Northern Spain would indicate that host specificity plays only a small part in structuring the macrofungal communities of these forests. Soil abiotic conditions, climatic influence, and physical factors of the forests (e.g. degree of patchiness of forest cover in region) are more likely to be the driving force behind the formation of macrofungal communities in Atlantic oak forests.

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APPENDIX 1

List of macromycetes found in the five plots during the three years of the project. Numbers refer to fruitbody counts. FG: Functional Group into which the fungal species were allocated. L, litter decay; M, ectomycorrhizal; P, parasitic; W, wood decay. Site codes: **A,** Abbeyleix; **K,** Kilmacrea; **R,** Raheen; **T,** Tomies; **U,** Union.

Species	FG	A	K	R	T	U
Amanita citrina Pers.	M	0	0	2	0	0
Amanita citrina var. *alba* (Gillet) E.-J. Gilbert	M	0	0	1	0	0
Amanita phalloides Fr.	M	0	0	1	0	0
Amanita rubescens (Pers.) Gray	M	0	0	1	0	0
Armillaria mellea (Vahl) P. Kumm.	P	2	34	1	0	3
Boletus badius Pers.	M	0	4	0	1	0
Boletus chrysenteron Bull.	M	3	0	0	0	0
Cantharellus cibarius Fr.	M	0	0	1	0	0
Clavulina coralloides (L.) J. Schröt.	L	1	0	0	0	0
Clavulina rugosa (Bull.) J. Schröt.	L	12	0	0	0	0
Clitocybe gibba (Pers.) P. Kumm.	L	0	1	0	0	0
Clitocybe vibecina (Fr.) Quél.	L	6	0	0	0	0
Collybia butyracea (Bull.) P. Kumm.	L	1	0	0	0	0
Collybia dryophila (Bull.) P. Kumm.	L	2	0	0	0	0
Cortinarius acutus (Pers.) Fr.	M	10	6	6	0	0
Cortinarius bolaris (Pers.) Fr.	M	0	0	5	0	0
Cortinarius flexipes Fr.	M	0	16	6	24	2
Cortinarius flexipes var. *inolens* H. Lindstr.	M	0	0	0	13	0
Cortinarius sanguineus (Wulfen) Fr.	M	0	0	1	0	0
Cortinarius stillatitius Fr.	M	0	0	3	1	0
Cortinarius umbrinolens P.D. Orton	M	0	0	0	1	0
Crepidotus mollis (Schaeff.) Staude	W	0	0	8	0	6
Crepidotus variabilis (Pers.) P. Kumm.	W	0	13	16	0	12
Entoloma conferendum (Britzelm.) Noordel.	M	0	1	7	0	0
Fistulina hepatica (Schaeff.) With.	P	2	0	0	0	0
Galerina marginata (Batsch) Kühner	L	3	0	0	0	0
Gymnopilus bellulus (Peck) Murrill	W	0	2	0	0	0
Hypholoma fasciculare (Huds.) P. Kumm.	W	0	0	4	19	0
Hypoxylon fragiforme (Scop.) J. Kickx	W	2	0	0	0	0
Hypoxylon fuscum (Pers.) Fr.	W	0	1	0	0	0
Inocybe langinosa Cooke	M	0	1	0	0	0
Inocybe napipes J.E. Lange	M	0	0	0	1	0
Kuhneromyces mutablis (Schaeff.) Singer & A.H. Sm.	W	0	0	18	0	0
Laccaria amethystina Cooke	M	37	17	12	50	16
Laccaria laccata (Scop.) Cooke	M	44	38	1	11	29
Lactarius camphoratus (Bull.) Fr.	M	0	0	0	1	0
Lactarius hepaticus Plowr.	M	0	0	0	6	0
Lactarius pyrogalus (Bull.) Fr.	M	0	1	0	0	0
Lactarius quietus (Fr.) Fr.	M	15	14	0	2	0
Lactarius rufus (Scop.) Fr.	M	0	2	0	0	0
Lactarius subdulcis (Pers.) Gray	M	0	0	1	0	0
Lactarius tabidus Fr.	M	1	0	0	5	0
Lactarius vietus (Fr.) Fr.	M	0	4	0	0	0
Leotia lubrica (Scop.) Pers.	L	0	0	9	6	0
Lycoperdon molle Pers.	L	0	0	5	0	0
Lycoperdon nigrescens Wahlenb.	L	1	0	34	0	4
Lycoperdon perlatum Pers.	L	0	0	35	2	1

Species	FG	A	K	R	T	U
Marasmiellus ramealis (Bull.) Singer	L	6	8	6	0	0
Marasmius androsaceus (L.) Fr.	L	12	2	13	0	0
Marasmius epiphylloides (Rea) Sacc. & Trotter	L	0	1	4	0	0
Marasmius hudsonii (Pers.) Fr.	L	24	1	20	1	0
Mycena aetites (Fr.) Quél.	L	0	5	1	0	0
Mycena alphitophora (Berk.) Sacc.	L	0	0	0	1	0
Mycena amicta (Fr.) Quél.	L	0	0	1	0	0
Mycena epipterygia (Scop.) Gray	L	0	3	0	0	0
Mycena erubescens Höhn.	L	0	0	0	0	1
Mycena filopes (Bull.) P. Kumm.	L	0	0	2	0	0
Mycena galopus (Pers.) P. Kumm.	L	6	8	3	0	13
Mycena galopus var. *candida* J.E. Lange	L	0	1	0	0	0
Mycena inclinata (Fr.) Quél.	L	1	0	0	0	0
Mycena leptocephala (Pers.) Gillet	L	3	1	1	0	0
Mycena metata (Fr.) P. Kumm.	L	0	0	3	0	7
Mycena polygramma (Bull.) Gray	L	0	0	1	2	0
Mycena pura (Pers.) P. Kumm.	L	0	0	1	0	0
Mycena stylobates (Pers.) P. Kumm.	L	0	1	0	0	0
Mycena vitilis (Fr.) Quél.	L	0	0	7	2	0
Neobulgaria pura (Pers.) Petr.	W	13	0	0	0	0
Panellus stipticus (Bull.) P. Karst.	W	0	0	13	1	0
Phallus impudicus L.	L	1	0	0	0	0
Pluteus cervinus (Schaeff) P. Kumm.	W	0	0	1	0	0
Psathyrella candolleana (Fr.) Maire	W	3	0	0	0	0
Psathyrella pennata (Fr.) Pearson & Dennis	L	0	3	0	0	0
Pseudoclitocybe cyathiformis (Bull.) Singer	W	0	0	0	8	0
Russula aeruginea Fr.	M	2	0	1	0	0
Russula atropurpurea (Krombh.) Britzelm.	M	2	0	0	0	0
Russula betularum Hora	M	0	0	0	6	0
Russula foetens (Pers.) Pers.	M	1	0	1	0	0
Russula illota Romagn.	M	0	4	0	0	0
Russula nobilis Velen.	M	0	1	1	0	0
Russula ochroleuca (Pers.) Fr.	M	9	18	3	5	0
Russula parazurea Jul. Schäff.	M	1	0	0	0	0
Rutstroemia firma (Pers.) P. Karst.	W	0	2	7	0	0
Rutstroemia sydowiana (Rehm) W.L. White	W	0	0	8	0	0
Scleroderma areolatum Ehrenb.	M	0	1	0	0	0
Scleroderma citrinum Pers.	M	92	1	0	0	0
Stereum hirsutum (Willd.) Pers.	W	6	6	21	10	8
Tapesia fusca (Pers.) Fuckel	W	0	1	0	0	1
Trametes versicolor (L.) Lloyd	W	0	0	0	0	1
Trichaptum abietinum (Dicks.) Ryvarden	W	0	0	1	0	0
Tricholoma album (Schaeff.) P. Kumm.	M	0	0	2	0	0
Tricholoma columbetta (Fr.) P. Kumm.	M	0	0	1	0	0
Tricholomopsis decora (Fr.) Singer	L	0	0	1	0	0
Xylaria carpophila (Pers.) Fr.	W	0	0	0	0	2
Xylaria hypoxylon (L.) Grev.	W	13	1	0	1	6
Xylaria sp.	W	1	0	0	1	0

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