The macrofungal component of biodiversity in Irish Sitka spruce forests

Richard O'Hanlon[a] and Thomas J. Harrington[a]

Abstract

Sitka spruce (*Picea sitchensis* (Bong.) Carr.) is the most commonly planted tree species in Ireland, with future increases in the area of Sitka spruce forests planned. In recent years the biodiversity of Sitka spruce plantations in Ireland has become a topic of much research interest. However, fungal biodiversity has yet to be systematically surveyed in Irish Sitka spruce forests. This study reports on the diversity of macrofungi from nine Sitka spruce plots in five counties surveyed over three years. One hundred and forty four species were discovered in the plots, including three species new (previously unrecorded) to the Republic of Ireland. Over half the species discovered were ectomycorrhizal species, highlighting the generalist nature of Sitka spruce as an ectomycorrhizal host in Western Europe. The 10 most common species are listed; members of the genus *Mycena* were the most commonly found macrofungi. On a relative sampling basis (species per m^2), the biodiversity of macrofungi in Irish Sitka spruce forests is comparable to that found in native Sitka spruce forests in Canada. The ability of Sitka spruce forests in Ireland to support native biodiversity is discussed with reference to studies of other taxonomic groups and recommendations for the promotion of fungal diversity in Irish Sitka spruce forests are made.

Keywords: *Diversity, ectomycorrhiza, decay, mushrooms, fungi*

Introduction

The word "biodiversity" has been defined in a variety of ways (more than 80 definitions in De Long 1996). In this article the definition used is that of the Convention on Biological Diversity (CBD): "Biological diversity means the variability among living organisms from all sources including, *inter-alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (Convention on Biological Diversity 1992). Biodiversity in this form is extremely difficult to measure and therefore only the organism diversity at the level of species is examined because it encompasses different hierarchies of biological and ecological diversity. Biodiversity is known to have large effects on ecosystem productivity and stability (Bolger 2001; Gaston and Spicer 2004; Hector 2011) and therefore its conservation is extremely important. Bullock et al. (2008) calculated that biodiversity is worth more than €700 million per annum to the Irish forest sector. The protection of biodiversity is also one of the key principles examined by the Forest Stewardship Council (FSC) in Ireland to ensure that forest produce complies with Sustainable Forest Management (SFM) practices.

[a] Corresponding author: Department of Life Sciences, University of Limerick, Limerick, Ireland (publications@rohanlon.org).

Fungal biodiversity worldwide has been estimated at over 1.5 million species (Hawksworth 1991) with forests being seen as having the highest fungal biodiversity of all ecosystems. Fungi hold key roles in the maintenance of forest ecosystems including: (i) nutrient cycling, retention and formation of soil structure, (ii) provision of food in detritivore food webs in forests and forest streams, (iii) micro-habitat creation in forests by fungal pathogens and (iv) mycorrhizal mutualisms (Moore et al. 2001). Historic under-recording of many groups of fungi in Ireland, especially forest fungi, has led to a situation where the Republic of Ireland is considered to have much fewer macrofungal records than similar countries (100 fewer than in Northern Ireland and 2200 fewer than in England; O'Hanlon and Harrington 2011). In 2007 the FUNCTIONALBIO project (Bolger et al. 2009) was established to investigate functional biodiversity in forests, including the diversity of soil decomposers and predatory and parasitic arthropods. The project investigated fungal biodiversity in Irish forests that contained native (ash, *Fraxinus excelsior* L.; and oak, *Quercus robur* L., Q. *petraea* L.) and non-native (Scots pine[1], *Pinus sylvestris* L.; and Sitka spruce, *Picea sitchensis* (Bong.) Carr.) tree species. The results for the fungal section of the project (O'Hanlon 2011) for Sitka spruce forests are summarised in this article.

Sitka spruce is native to the west coast of North America, its range stretching along the coast from Prince William Sound in Alaska, south to Casper, California (Peterson et al. 1997). It is a light demanding tree, which grows well in moist fertile soils. In general, Sitka spruce forests are not intensively managed in North America. These Sitka spruce forests are characterised by having high tree species diversity, lush understory and shrub layers, and large amounts of coarse woody debris (CWD), especially fallen trees. In contrast, Sitka spruce forests in Ireland and the remainder of Europe are usually intensively managed. Low tree species and understory species diversity (French et al. 2008), short rotation lengths (Joyce and O'Carroll 2002), and low levels of CWD (Sweeney et al. 2010a) characterise Sitka spruce plantations in Ireland. Sitka spruce is the most commonly planted tree species in Ireland (National Forest Inventory 2007) and the United Kingdom (National Forest Inventory 2003). Sitka spruce now accounts for over 50% of the forested land in Ireland (National Forest Inventory 2007), with plans to increase this to over 60% by 2030 (Department of Agriculture, Food and Forestry 1996); therefore information regarding the effect of Sitka spruce plantations on native fungal biodiversity is important to inform future management of Sitka spruce plantations.

The objective of this study was to investigate macrofungal species richness (number of species) and functional group richness (number of species within specified functional groups) in Irish Sitka spruce forests. Comparisons of the results from this study with those from other non-native and native Sitka spruce forests were expected to reveal lower species richness in non-native forests, related to other major differences between non-native and native Sitka spruce forests (e.g. lower tree species diversity, lower vascular plant diversity, shorter rotation times, less CWD).

[1] There is some debate among experts as to whether or not Scots pine is native to Ireland, with the majority being of the view that it is a naturalized species.

Table 1: *Descriptions of the nine Sitka spruce forests surveyed in this study. The tree species present inside the plot, apart from Sitka spruce, are listed. Soil description was taken from the geological maps of Ireland (Gardener and Radford 1980). Characterization of the vegetation in the plots based on the Fossitt (2000) habitat scheme reflected the conifer plantation habitat type (WD4, forest with a broadleaf component of less than 25% and where the overriding purpose of the forest is commercial timber production).*

Plot name	County	Tree species present	Stand age	Soil type	Parent material
Ballygawley	Sligo	Qp	40	Lithosol	Granite and sandstone
Bohatch	Clare	Pa	30	Blanket peat	Basin peat
Chevy chase mature	Clare	-	40	Gley	Sandstone
Chevy chase young	Clare	Bp	20	Gley	Sandstone
Cloonagh	Sligo	-	18	Grey brown podzol	Limestone
Dooary	Laois	-	24	Gley	Carboniferous shale
Moneyteige	Wicklow	-	35	Peaty podzol	Granite and sandstone
Quitrent	Cork	Pc	28	Gley	Sandstone
Stanahely	Wicklow	-	25	Peaty podzol	Granite and sandstone

Tree species abbreviations: Qp, Quercus pertaea L.; Pa, Picea abies (L.) Karst.; Bp, Betula pubescens Ehrh.; Pc, Pinus contorta Dougl. ex. Loud.; -, few or no other tree species present.

Methods

Plot selection

Nine Sitka spruce sites were chosen (Table 1) from a list previously used by the BIOFOREST study (Smith et al. 2005; Iremonger et al. 2006; Smith et al. 2006). As much as was possible we tried to select pure (100%) Sitka spruce stands, although budget and time restrictions meant that some of the sites selected were mixed tree species stands. The stands ranged in age from 18 to 40-years-old. 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 ground and large distance to forest edge).

Macrofungal sampling

The plots were visited at least twice in the autumn (August-November) of 2007, 2008 and 2009. All macrofungi inside the plots were identified *in situ* where possible, and sporocarps (mushrooms) of unidentified species were retained for later identification according to a standard approach (Courtecuisse and Duhem 1995). We defined macrofungi as fungi which are visible to the naked eye and generally produce sporocarps greater than 5 mm in diameter. 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 et al. 2000). The microfungi, such as slime molds, rusts and smuts could not be examined using this approach. Similarly, some mycorrhizal groups (including arbuscular, ericoid and ectendomycorrhizal types) could not be sampled using this method. The functional groups used here are slightly arbitrary in that it is known that many fungi can switch between these functional groups depending on environmental conditions. Many species can be facultatively ectomycorrhizal, switching to decomposer lifestyles under certain conditions (Talbot et al. 2008; but see Baldrian 2009); while other decomposer species also function as weak parasites (e.g. honey fungus *Armillaria mellea*). However, the examination of functional group diversity is still of interest as it can highlight differences in the macrofungal communities of different forest types.

We examined the species richness and functional group richness of fungi in the Sitka spruce 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 Sitka spruce forests in the Republic of Ireland.

Results

Species richness patterns

A total of 144 macrofungal species were recorded in the Sitka spruce plots. Three species, previously unrecorded in the Republic of Ireland species list were found within the plots during this project, namely *Ophiocordyceps forquignonii*, *Cortinarius evernius* and *Elaphocordyceps longisegmentis*. The number of species recorded increased over the three years of the study (Figure 1). There was no macrofungal species ubiquitous to all plots (Table 2). *Mycena* was the most species rich genus, followed by *Cortinarius*, *Russula* and *Lactarius* with 19, 13, 11 and 9 species, respectively. Despite the high species richness of some genera, more than half (57%) of the species were found only once over the three years.

Functional group richness patterns

From a functional group point of view, 44%, 29%, 24% and 3% species could be classed as ECM, WD, LD and P species respectively (Figure 2). Of the 10 most widely distributed litter decay fungi, seven were of the genus *Mycena* (*M. vitilis, M. metata, M. leptocephala, M. rorida, M. filopes, M. stylobates* and *M. epipterygia*). The remaining three litter decay species were the wrinkled club (*Clavulina rugosa*), the earthy powdercap (*Cystoderma amianthinum*) and the puffball (*Lycoperdon nigrescens*). The most widely distributed ectomycorrhizal species included five

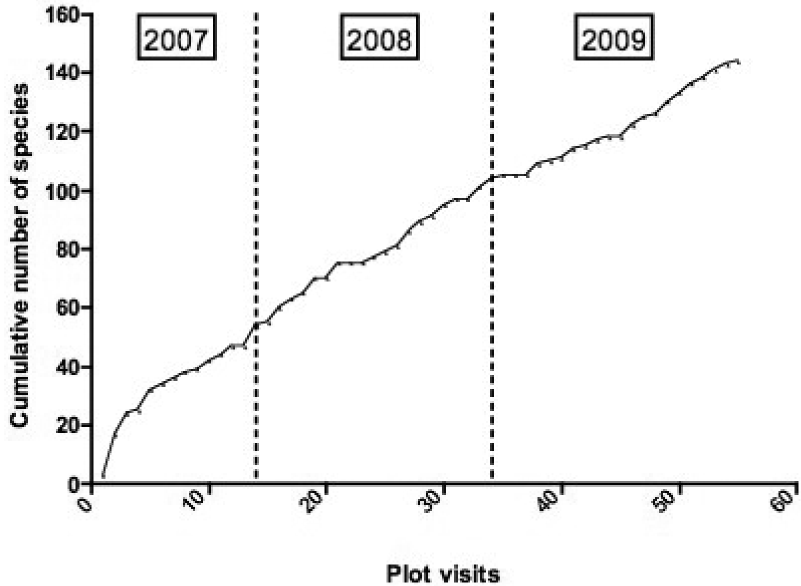

Figure 1: *Cumulative number of macrofungal species recorded over the duration of the study. The years of the study are separated by vertical dashed lines.*

Cortinarius species (*C. cinnamomeous*, *C. obtusus*, *C. anomalus*, *C. acutus* and *C. flexipes*), two *Laccaria* species (*L. laccata* and *L. amethystina*), two *Russula* species (*R. ochroleuca* and *R. emetica*) and the blusher (*Amanita rubescens*). *Heterobasidion annosum* was the only parasitic fungus that was present in more than one plot. Only three wood decay species (*Hypholoma fasciculare*, *Postia caesia* and *Calocera viscosa*) were present in more than four plots.

Abundant and edible macrofungal species

Further details are provided below for macrofungal species that were either (i) very prolific (producing large biomass) species or (ii) species that produce edible sporocarps.

(i) Prolific species in the plots were *Hemimycena gracilia*, *Mycena leptocephala*, *Russula ochroleuca*, *Hypholoma fasciculare*, *Rhodocollybia butyracea*, *Clavulina rugosa* and *Laccaria laccata*. More than 100 sporocarps of these species were recorded from all of the plots (per 900 m^2) over the three years of the study. *Russula ochroleuca*, *Mycena leptocephala*, *Hypholoma fasciculare*, *Laccaria laccata*, and *Rhodocollybia butyracea* were found in more than four of the plots, while *Clavulina rugosa* and *Hemimycena gracilis* were abundant, but found in less than four of the plots.

(ii) Of the edible macrofungal species found in the plots, those that are highly rated by the culinary industry, and were also prolific include the cep *Boletus edulis*,

Table 2: *The most commonly found macrofungal species in the plots, based on the number of plots (and percentage in parenthesis) in which these species were recorded. The functional group (based on primary mode of nutrition) of the species is also given.*

Species	No of plots	Functional Group
Mycena leptocephala	7 (78%)	LD
Laccaria laccata	7 (78%)	ECM
Hypholoma fasciculare	7 (78%)	WD
Mycena vitilis	7 (78%)	LD
Mycena metata	7 (78%)	LD
Russula ochroleuca	5 (56%)	ECM
Laccaria amethystina	5 (56%)	ECM
Mycena rorida	5 (56%)	LD
Postia caesia	5 (56%)	WD
Calocera viscosa	4 (44%)	WD

Abbreviations: LD, litter decay; ECM, ectomycorrhizal; WD, wood decay.

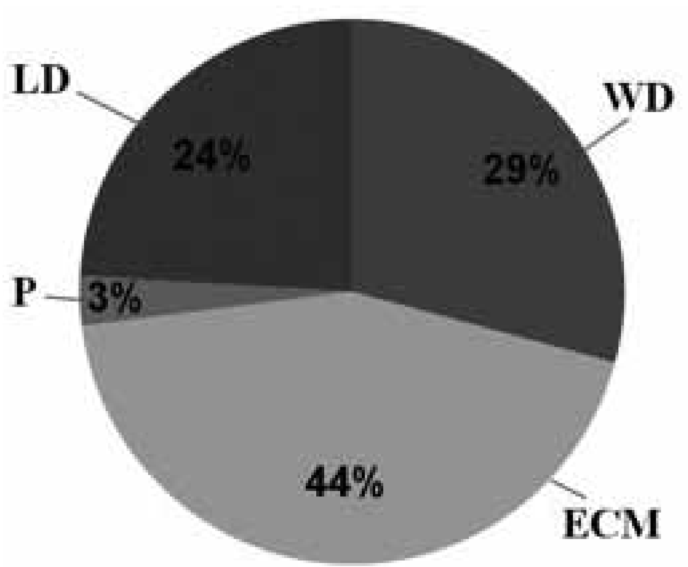

Figure 2: *Functional group breakdown of the macrofungal species (n=144) found in the plots. LD, litter decay; ECM, ectomycorrhizal; P, parasitic; and WD, wood decay species.*

the autumn chanterelle *Cantharellus tubaeformis*, the chanterelle *C. cibarius* and the false saffron milkcap *Lactarius deterrimus*. In particular the autumn chanterelle and false saffron milkcap were found in areas composed of pure Sitka spruce with no other tree species within 5 m, and often in large quantities. *Cantharellus cibarius* was more common near birch trees within a Sitka spruce stand, such as in the younger Chevy chase stand.

Discussion

The fungal biodiversity of Sitka spruce forests in Ireland and other regions

To the authors' knowledge, this is the first systematic macrofungal biodiversity study of Irish Sitka spruce forests. As it was conducted over a relatively short time period (three years), the study may not have revealed the full extent of macrofungal diversity in Sitka spruce forests in Ireland, and further surveying would undoubtedly reveal more new species in these plots. However, work in Britain by Ferris et al. (2000) has shown that up to 80% of the expected macrofungal species are likely to be revealed from three years of intensive sampling, thus supporting the validity of the data collected in this study. Unfortunately however, there are some limitations to the design of this study, a drawback common to most survey studies of this kind. Tree species present (some mixed species stands and some monoculture stands), stand age (stands ranging in age from 18 to 40-years-old), and stand management factors (mixture of thinned and unthinned stands) were confounded, so it is difficult to be definitive as to which site factors had the greatest impact on macrofungal diversity. Nevertheless, this study does provide baseline data that may inform future studies, while also yielding new macrofungal species records for five counties in the Republic of Ireland. Heslin et al. (1992) and Dowding and Smith (2008) have listed some macrofungal species found in Irish Sitka spruce forests. However, the first study by Heslin et al. (1992) was more focused on the below-ground ectomycorrhizal morphotype diversity; while the work by Dowding and Smith (2008) only listed edible and poisonous species. That so many fungal species were found in Sitka spruce forests lends weight to O'Hanlon and Harrington's (2011) hypothesis that much of Ireland's undiscovered fungal biodiversity may be found in forest habitats. It is likely that more new macrofungal species will be discovered if these plots are sampled more intensively in the future. New species were found at regular intervals over a 20-year sampling period in macrofungal studies conducted in forests in Britain and Switzerland (Tofts and Orton 1998; Straatsma and Krisai-Greilhuber 2003). Two of the main reasons for the increasing macrofungal species richness over time in forests are (i) omission of species at sampling due to the sporadic nature of macrofungal fruiting (Krebs et al. 2008) and (ii) changes in the macrofungal community as the forest ages (Smith et al. 2002; Kranabetter et al. 2005). Taking these difficulties into account, it is probable that even with almost constant sampling of a forest macrofungal community, the true species richness of the community may never be revealed using sporocarp-only studies. Another negative aspect of using sporocarps as indicators of ectomycorrhizas is the low similarity between above-ground sporocarp presence and below-ground presence of the ectomycorrhizas (Horton and Bruns 2001). Difficulties aside, sporocarp studies continue to be used to examine fungal ecology and phenology in forest ecosystems (Ferris et al. 2000; Humphrey et al. 2003; Roberts et al. 2004; Kranabetter et al. 2005; Buee et al. 2011). One of the main benefits of sporocarp studies, apart from the ease of data collection, is that only the ectomycorrhizal species active in the ecosystem are recorded. Ectomycorrhizas are dependent on host carbon for the production of sporocarps in natural ecosystems (Högberg et al. 2001); therefore sporocarp presence is directly related to activity in the ecosystem.

The findings of this study agree with previous work in Scotland which indicates that Sitka spruce is an ectomycorrhizal generalist, capable of forming ectomycorrhizas with many native fungi (Alexander and Watling 1987). An interesting phenomenon, known as "host shift" (Watling 1995), can occur when a native fungal species is found in stands of non-native tree species. The ectomycorrhizal species, *Cortinarius rubellus*, is known to have shifted host from its native habitat of Scots pine to plantation Sitka spruce forests in Britain and Ireland. Once thought to be restricted to native pine forests in Scotland, it is now found in Sitka spruce forests in Britain (Watling 1982) and Ireland (Harrington 1994). This macrofungal species spreads by both windblown spores and by underground mycelia. Two scenarios which may explain its presence in plantation Sitka spruce forests are that (i) it was present in a nearby pine stand and entered the plantation from windblown spores, or (ii) the plantation was previously a pine forest and existing mycelia propagules of the fungus remained in the soil after pine harvest to colonise the newly planted forest. Moreover, work in Britain by Humphrey et al. (2003) has shown that distance to nearest existing native pine wood is positively related to the number of rare pine wood macrofungal species found in Sitka spruce plantations.

The large number and quantity of edible macrofungal species found in Sitka spruce forests suggest that the findings may be of economic significance. Smith (2001) estimated that Ireland imports €2 million worth of wild mushrooms per annum. Currently, work is being carried out to investigate the production of wild edible fungi in Irish forests, including Sitka spruce forests (Harrington et al. 2009), and this may reveal even more information about edible fungal species in this forest type. Of the economically damaging fungi found, *Heterobasidion annosum* is the most serious disease of Sitka spruce in Ireland (Joyce and O'Carroll 2002). It and other fungal pathogens are known to infect through cut surfaces of trees (Dowding 1970) and if no preventative measures are taken large economic losses can be expected.

The results of this study show that stands of Sitka spruce in Ireland have more macrofungal species richness (species per m^2) than native Sitka spruce forests in Canada (Outerbridge 2002), yet not as rich as Sitka spruce plantations in Britain (Humphrey et al. 2003) (Table 3). In fact, the fungal biodiversity of Sitka spruce forests in Ireland was found to be as high as native Irish oak forests (O'Hanlon and Harrington, unpublished data). There were strong similarities between Sitka spruce forests in different locations in respect of certain biodiverse genera. *Mycena*, *Cortinarius* and *Russula* were found to be very species rich in this survey (19, 13 and 11 species) and in similar studies from Britain (28, 35 and 16 species) (Humphrey et al. 2003) and Canada (22, 14 and 13 species) (Roberts et al. 2004). There were, however, large differences in the functional group richness of the species found in Sitka spruce

Table 3: *Fungal species richness (number of species) and species per m² in Sitka spruce forests in Ireland, Britain and Canada. The numbers in parenthesis in column 2 indicate the percentage of the total number of species that were found only in Sitka spruce forests.*

Region	Species richness	Species/m²	Source
Ireland	144 (53%)	0.16	This study
Britain	269 (37%)	0.21	Humphrey et al. 2003
Canada	127 (41%)	0.15	Outerbridge 2002

forests in the different regions. Similar to Irish forests, British forests had 41% of the total species richness from the ectomycorrhizal functional group (Humphrey et al. 2003). The ectomycorrhizal functional group richness of Canadian forests was much lower, at just 28% (Outerbridge 2002).

The macrofungal aspect

Although confounding effects in this study design diminish its ability to make conclusions regarding the relationship between macrofungal species richness and site factors, previous research results in the U.K. (Humphrey et al. 2003) and North America (Jones et al. 2003; Luoma et al. 2006) have indicated that fungal biodiversity in managed forests may be increased through: (i) the retention of mature trees after final harvesting, (ii) increasing the amounts and quality of CWD left on site and (iii) through mixed tree species planting. These recommendations are similar to those given for increasing biodiversity of other taxonomic groups in forests (Table 4). Ectomycorrhizal fungi in particular are known to be negatively affected by clear cutting (Jones et al. 2003). Ectomycorrhizas rely on the host tree for a food source, therefore when the host is removed the fungus cannot survive (Hogberg et al. 2001). Retention of mature trees in swathes rather than as single stems has been found to be more beneficial to fungal biodiversity (Luoma et al. 2006). Old growth forests are known to support a different community of macrofungi to young forests (Smith et al. 2002; Kranabetter et al. 2005), therefore retention of mature swathes of forest would also provide a habitat for these old-growth fungal communities to survive in. Increasing the amount and quantity of CWD left on site after harvesting provides a suitable habitat for wood decay fungi. Research in Britain found that the number of wood decay fungal species is positively related to the amount of CWD in the forest (Ferris et al. 2000). Previous research has showed that there is a positive relationship between tree species richness and fungal species richness (Schmit et al. 2005; Ferris et al. 2000). Ectomycorrhizal fungi can be quite specific in the tree species which they form relationships with (Molina et al. 1992), while many decay fungi are restricted in the litter and wood which they can decompose (Ludley et al. 2008). The ectomycorrhizal specificity and preferences of decay fungi both contribute to specific communities of fungi being found in forests, and these communities are related to the dominant tree species of the forest (Buee et al. 2011; O'Hanlon and Harrington, unpublished data).

The results of this study have shown that Sitka spruce forests in Ireland can support high fungal species richness. Similarly, the biodiversity of other taxa in Irish Sitka spruce forests can be encouraged, as summarised in Table 4. The biodiversity of the insect groups (Table 4) can be increased through retention of mature trees, increasing the amounts of CWD retained and through the provision of more open spaces in the forest stand (Oxbrough et al. 2006, 2010; Gittings et al. 2006; Arroyo et al. 2010). More open spaces also results in increased bird biodiversity (O'Halloran et al. 1998; Wilson et al. 2010; Sweeney et al. 2010b). The promotion of structural heterogeneity, increased volume of CWD in the later stages of decay, and planting of mixed (especially coniferous/broadleaf) tree species forests have been identified as methods for increasing vascular plant biodiversity in Sitka spruce plantations (French et al. 2008). Epiphyte biodiversity can also be increased through the retention of mature patches of plantation forests and the planting of more mixed tree species (especially broadleafed) at the stand level (Coote et al. 2008). The parameters identified as important for increasing the biodiversity of the different taxonomic groups (Table 4) are now requirements of the Forest Biodiversity Guidelines (Forest Service 2000). Parameters would also have a positive effect on fungal biodiversity in Irish forests.

Table 4: *Management parameters identified as important for promoting biodiversity in Sitka spruce forests in Ireland. Column 2 lists the number of species found in Sitka spruce forests for that group and the percentage (in parenthesis) of Ireland's total species richness for that species group.*

		Importance for increasing biodiversity				
Taxonomic group	**Species richness**	**OS**	**MT**	**SW**	**CWD**	**TD**
Spiders[1]	154 (13%)[6]	√	√	x	x	x
Hoverflies[1]	50 (25-50%)[7]	√	x	√	√	x
Beetles[2]	47 (2%)[6]	√	√	x	x	x
Birds[3]	21 (9%)[6]	√	x	x	√	x
Vascular plants[1]	167 (7%)[6]	√	x	x	√	√
Epiphytes[4]	68 (4%)[6]	x	√	x	x	√
Fungi[5]	144 (14%)[8]	x	√	x	√	√

√, effective; x, not effective, less important or undetermined.

Abbreviations: OS, provision of open spaces in the stand; MT, retention of mature trees after harvesting; SW, provision of areas with standing water in the stand; CWD, provision of coarse woody debris of high quality and quantity after thinning/harvesting; TD, increasing tree species diversity at the stand level.

Sources: 1, Smith et al. (2006); 2, Oxbrough et al. (2010); 3, Sweeney et al. (2010b); 4, Coote et al. (2008); 5, O'Hanlon (2011); 6, NBDC (2010); 7, Speight et al. (2006), as cited in Keil et al. (2008); 8, O'Hanlon and Harrington (2011).

Conclusions

The *Biodiversity in Britain's planted forests* project (Humphrey et al. 2003) arrived at similar conclusions to those given in this paper – biodiversity in Sitka spruce forests can be increased through the retention of mature forest patches and increasing tree species diversity. Related research in Britain has identified exotic tree species plantations as having an important part to play in the conservation of native taxonomic groups, by providing a complementary habitat for those groups (Quine and Humphrey 2010). Sitka spruce plantations in particular are capable of supporting native biodiversity, especially if more stands are allowed to reach old-growth conditions (Humphrey 2005), and these forests could also be managed to provide a supplementary habitat for native fungal biodiversity in Ireland.

Acknowledgements

The authors would like to acknowledge the Council for Forest Research and Development (COFORD) funding for this research through the FUNCTIONALBIO project. Prof. Tom Bolger is acknowledged for the management of the FUNCTIONALBIO work package. The comments provided by the editors and an anonymous reviewer have greatly improved the manuscript and are acknowledged.

References

Alexander, I. and Watling, R. 1987. Macrofungi of Sitka spruce in Scotland. *Proceedings of the Royal Society of Edinburgh* 93: 107-115.

Arroyo, J., Moraza, M.L. and Bolger, T. 2010. The mesostigmatid mite (*Acari*, *mesostigmata*) community in canopies of Sitka spruce in Ireland and a comparison with ground moss habitats. *Graellsia* 66: 29-37.

Baldrian, P. 2009. Ectomycorrhizal fungi and their enzymes in soils: is there enough evidence for their role as facultative soil saprotrophs? *Oecologia* 161: 657-660.

Bolger, T. 2001. Functional value of species biodiversity. *Biology and Environment: Proceedings of the Royal Irish Academy* 101: 199-224.

Bolger, T., Kenny, J., Harrington, T.J., O'Hanlon, R., Arroyo, J., Anderson, A. and Keithe, A. 2009. *The FUNCTIONALBIO* Project. http://www.coford.ie/researchprogramme/thematicareapolicyandpublicgoods/forestbiodiversity/functionalbio/

Buee, M., Maurice, J.P., Zeller, B., Andrianarisoa, S., Ranger, J., Courtecuisse, R., Marçais, B. and Le Tacon, F. 2011. Influence of tree species on richness and diversity of epigeous fungal communities in a French temperate forest stand. *Fungal Ecology* 4: 22-31.

Bullock, C., Kretsch, C. and Candon, E. 2008. *The Economic and Social Aspects of Biodiversity.* http://www.environ.ie/en/Heritage/PublicationsDocuments/FileDownLoad,17321,en.pdf

Convention on Biological Diversity. 1992. The Convention on Biological Diversity. http://www.cbd.int/doc/legal/cbd-en.pdf

Coote, L., Smith, G.F., Kelly, D.L., O'Donoghue, S., Dowding, P., Iremonger, S. and Mitchell, F.J.G. 2008. Epiphytes of Sitka spruce (*Picea sitchensis*) plantations in Ireland and the effects of open spaces. *Biodiversity and Conservation* 17: 953–968.

Courtecuisse, R. and Duhem, B. 1995. *Mushrooms and Toadstools of Britain and Europe*. Harper Collins, London.

De Long, D.C. 1996. Defining biodiversity. *Wildlife Society Bulletin* 24: 738-749.

Department of Agriculture, Food and Forestry. 1996. *Growing for the future. A strategic plan for the development of the forestry sector in Ireland*. Department of Agriculture, Food and Forestry, Dublin.

Dowding, P. 1970. Colonization of freshly bared pine sapwood surfaces by staining fungi. *Transactions of the British Mycological Society* 55: 399-412.

Dowding, P. and Smith, L. 2008. *Forest Fungi in Ireland*. COFORD, Dublin.

Ferris, R., Peace, A.J. and Newton, A.C. 2000. Macro fungal communities of low land Scot's pine and Norway spruce plantations in England: relationships with site factors and stand structure. *Forest Ecology and Management* 131: 255-267.

Forest Service. 2000. Forest biodiversity guidelines. Department of Marine and Natural resources. http://www.agriculture.gov.ie/forestry/publications/biodiversity.pdf

Fossitt, J.A. 2000. *A guide to habitats in Ireland*: http://www.heritagecouncil.ie/publications/habitats/Guide_to_Habitats.pdf

French, L.J., Smith, G.F., Kelly, D.L., Mitchell, F.J.G., O'Donoghue, S., Iremonger, S.F. and McKee, A. 2008. Ground flora communities in temperate oceanic plantation forests and the influence of silvicultural, geographic and edaphic factors. *Forest Ecology and Management* 255: 476-494.

Gardener, M.J. and Radford, T. 1980. *Soil Associations of Ireland and Their Land Use Potential*. Dublin, Ireland: An Foras Talúntais.

Gaston, K.J. and Spicer, J.I. 2004. *Biodiversity: an Introduction*. Blackwell publishing, Oxford.

Gittings, T., O'Halloran, J., Kelly, T. and Giller, P.S. 2006. The contribution of open spaces to the maintenance of hoverfly (*Diptera, Syrphidae*) biodiversity in Irish plantation forests. *Forest Ecology and Management* 237: 290–300.

Harrington, T.J. 1994. New Irish fungal records. *Irish Naturalists' Journal* 24: 413-414.

Harrington, T.J., Cullen, M., O'Connell, J., Spazzi, J., Connolly, K., Fallon, D. and O'Dea, B. 2009. *The FORESTFUNGI project*: http://www.coford.ie/researchprogramme/thematicareaharvestingandproducts/non-woodproducts/forestfungi/

Hawksworth, D.L. 1991. The fungal dimension of biodiversity: magnitude, significance, and conservation. *Mycological Research* 95: 641–655.

Hector, A. 2011. Diversity favours productivity. *Nature* 472: 45-46.

Heslin, M.C., Blasius, D., McElhinney, C. and Mitchell, D.T. 1992. Mycorrhizal and associated fungi of Sitka spruce in Irish forest mixed stands. *European Journal of Forest Pathology* 22: 46-57.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A.F.S., Ekblad, A., Högberg, M.N., Nyberg, G., Ottosson-Lofvenius, M. and Read, D.J. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411: 789–792.

Horton, T.R. and Bruns, T.D. 2001. The molecular revolution in ectomycorrhizal ecology: Peeking into the black-box. *Molecular Ecology* 10: 1855-1871.

Humphrey, J.W. 2005. Benefits to biodiversity from developing old-growth conditions in British upland spruce plantations: a review and recommendations. *Forestry* 78: 33-53.

Humphrey, J.W., Ferris, R. and Quine, C. 2003. *Biodiversity in Britain's Planted Forests*. The Forestry commission, Edinburgh.

Iremonger, S., Gittings, T., Smith, G.F., Wilson, M.W., Oxbrough, A., Coote, L., Pithon, J., O'Donoghue, S., McKee, A., O'Halloran, J., Kelly, D.L., Giller, P.S., O'Sullivan, A., Neville, P., Mitchell, F.J.G., O'Donnell, V., Kelly, T.C. and Dowding, P. 2006. *Investigation of Experimental Methods to Enhance Biodiversity in Plantation Forests*. BIOFOREST Project 3.1.3 Final Report to COFORD:

http://bioforest.ucc.ie/pages/project_three.htm
Jones, M.D, Durall, D.M. and Cairney, J. 2003. Ectomycorrhizal fungal communities in young forest stands regenerating after clearcut logging. *New Phytologist* 157: 399-422.

Joyce, P. and O'Carroll, N. 2002. *Sitka Spruce in Ireland*. COFORD, Dublin.

Keil, P., Dziock, F. and Storch, D. 2008. Geographical patterns of hoverfly (*Diptera, Syrphidae*) functional groups in Europe: inconsistency in environmental correlates and latitudinal trends. *Ecological Entomology* 33: 748-757.

Kranabetter, J.M., Friesen, J., Gamiet, S. and Kroeger, P. 2005. Ectomycorrhizal mushroom distribution by stand age in western hemlock – lodgepole pine forests of northwestern British Columbia. *Canadian Journal of Forest Research* 35: 1527–1539.

Krebs, C.J., Carrier, P., Boutin, S., Boonstra, R. and Hofer, E. 2008. Mushroom crops in relation to the weather in southwestern Yukon. *Botany* 86: 1497-1502.

Ludley, K.E., Robinson, C.H., Jickell, S., Chamberlain, P.M. and Whitaker, J. 2008. Differential response of ectomycorrhizal and saprotrophic fungal mycelium from coniferous forest soils to selected monoterpenes. *Soil Biology and Biochemistry* 40: 669–678.

Luoma, D.L., Eberhart, J.L., Molina, R. and Stockdale, C.A. 2006. The spatial influence of Psuedotsuga menziessi retention trees on ectomycorrhizal diversity. *Canadian Journal of Forest Research* 36: 2651-2573.

Molina, R.J., Massicotte, H.B. and Trappe, J.M. 1992. Specificity phenomena in mycorrhizal symbioses: Community-ecological consequences and practical implications. In *Mycorrhizal Functioning, an Integrative Plant-fungal Process*. Ed. Allen, M.F., New York. Routledge, Chapman and Hall, pp. 357–423.

Moore, D., Nauta, M., Evans, S. and Rotheroe, M. 2001. *Fungal Conservation- Issues and Solutions*. Cambridge University Press, Cambridge.

National Forest Inventory. 2003. *National inventory of woodland and trees: Great Britain*. The Forestry Commission, Edinburgh.

National Forest Inventory. 2007. *National Forest Inventory of Ireland*:
http://www.agriculture.gov.ie/index.jsp?file=forestry/NFI/NFI_results.xml

NBDC. 2010. Data Centre Mapping System: http://maps.biodiversityireland.ie/

O'Halloran, J., Walsh, P.M., Giller, P.S., Kelly, T.C. and Duffy, B.L. 1998. An assessment of avian biodiversity and opportunities for enhancement in Irish forests: preliminary results. 55: 2-14.

O'Hanlon, R. 2011. The Diversity of Fungi in Four Irish Forest Types. Unpublished Ph.D. Dissertation, University of Limerick, Ireland.

O'Hanlon, R. and Harrington, T.J. 2011. Diversity and distribution of mushroom-forming fungi (Agaricomycetes) in Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy* 111B. DOI: 10.3318/ BIOE.2011.111.10.

Outerbridge, R.A. 2002. *Macrofungus Ecology and Diversity under Different Conifer Monocultures on Southern Vancouver Island*. Unpublished Ph.D. Dissertation, University of Victoria, BC.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S. and Kelly, T.C. 2006. The influence of open space on ground-dwelling spider assemblages within plantation forests. *Forest Ecology and Management* 237: 404-417.

Oxbrough, A.G., Irwin, S., Kelly, T.C. and O'Halloran, J. 2010. Ground-dwelling invertebrates in reforested conifer plantations. *Forest Ecology and Management* 259: 2111–2121.

Peterson, E.B., Peterson, N.M., Weetman, G.F. and Martin, P.J. 1997. *Ecology and management of Sitka spruce, emphasizing its natural range in British Columbia*. University of British Columbia, Vancouver, B.C.

Quine, C.P. and Humphrey, J.W. 2010. Plantations of exotic tree species in Britain: irrelevant for biodiversity or novel habitat for native species? *Biodiversity and Conservation* 19: 1503–1512.

Roberts, C., Ceska, O., Kroeger, P. and Kendrick, B. 2004. Macrofungi from six habitats over five years in Clayoquot Sound, Vancouver Island. *Canadian Journal of Botany* 82: 1518–1538.

Schmit, J.P., Mueller, G.M., Leacock, P.R., Mata, J.L., Wu, Q. and Huang, Y. 2005. Assessment of tree species richness as a surrogate for macrofungal species richness. *Biological Conservation* 121: 99–110.

Smith, G.F., Gittings, T., Wilson, M.W., French, L., Oxbrough, A., O'Donoghue, S., Pithon, O'Donnell, V., McKee, A.M., Iremonger, S., O'Halloran, J., Kelly, D.L., Mitchell, F.J.G., Giller, P.S. and Kelly, T. 2005. *Assessment of Biodiversity at Different Stages of the Forest Cycle*. BIOFOREST Project 3.1.2 Final Report to COFORD: http://bioforest.ucc.ie/pages/project_two.htm

Smith, G.F., Gittings, T., Wilson, M.W., Oxbrough, A., Iremonger, S., O'Donoghue, S., McKee, A.M., O'Halloran, J., Kelly, D.L., Pithon, J., O'Sullivan, A., Neville, P., Mitchell, F.J.G., Giller, P.S., O'Donnell, V. and Kelly, T.C. 2006. *Biodiversity Assessment of Afforestation Sites*. BIOFOREST Project 3.1.1 Final Report to COFORD: http://www.coford.ie/iopen24/pub/pub/Reports/BIOFOREST312text.PDF

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

Smith, L. 2001. *Wild Edible Forest Mushrooms of Ireland*. Unpublished Masters Thesis, Galway-Mayo Institute of Technology.

Speight, M.C.D., Castella, E., Sarthou, J.P. and Monteil, C. 2006. Syrph the Net, the Database of European Syrphidae. Syrph the Net publications, Dublin.

Straatsma, G. and Krisai-Greilhuber, I. 2003. Assemblage structure, species richness, abundance, and distribution of fungal fruiting bodies in a seven year plot-based survey near Vienna. *Mycological Research* 107: 632-640.

Sweeney, O.F., Martin, R.D., Irwin, S., Kelly, T.C., O'Halloran, J., Wilson, M.W. and McEvoy, P.M. 2010a. A lack of large-diameter logs and snags characterises dead wood patterns in Irish forests. *Forest Ecology and Management* 259: 2056-2064.

Sweeney, O.F., Wilson, M.W., Irwin, S., Kelly, T.C. and O'Halloran, J. 2010b. Are bird density, species richness and community structure similar between native woodlands and non-native plantations in an area with a generalist bird fauna? *Biodiversity and Conservation* 19: 2329–2342.

Talbot, J.M., Allison, S.D. and Treseder, K.K. 2008. Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change. *Functional Ecology* 22: 955–963.

Tofts, R.J. and Orton, P.D. 1998. The species accumulation curve for agarics and boleti from a Caledonian pine wood. *Mycologist* 12: 98-102.

Watling, R. 1982. Cortinarius speciosissimus: the cause of renal failure in two young men. *Mycopathologia* 79: 71–78.

Watling, R. 1995. Assessment of fungal diversity: macromycetes, the problems. *Canadian Journal of Botany* (Suppl. 1) 73: S15-S24.

Wilson, M.W., Gittings, T., Kelly, T.C. and O'Halloran, J. 2010. The importance of non-crop vegetation for bird diversity in Sitka spruce plantations in Ireland. *Bird Study* 57: 116-120.