Spatial and Temporal Aspects of Macrofungal Community Structure

Aqilah Mohammad

School of Biological Sciences
Royal Holloway, University of London
Egham, Surrey, TW20 0EX
United Kingdom

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Declaration of Authorship

These doctoral studies were conducted under the supervision of Prof. Alan C. Gange.
The work presented in this thesis is the result of original research carried out by myself, whilst enrolled in the School of Biological Sciences as a candidate for the degree of Doctor of Philosophy. This work was conducted independently and has not been submitted for any other degree of award in any other university or educational establishment. Where I have consulted the work of others, this is always clearly stated.

Aqilah Mohammad
May 2013

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Abstract

The thesis contains an analysis of spatial and temporal aspects of macrofungal fruiting. In total, the thesis contains 8 chapters with 5 experimental chapters. These chapters involved studies of i) fungal phenology (Chapter 3), ii) fungal-host associations (Chapter 4), iii) the relationship between fungi and climatic variables (Chapter 5), iv) seasonal dynamics of fungal interactions (Chapter 6) and v) fungal species co-occurrence patterns (Chapter 7). Most data, analysed in the studies of phenology, host associations and influences of climate on fungi were obtained from a long term fungal dataset with records gathered by local mycologist, Edward G. Gange from more than 1000 localities within a 30 km radius of Salisbury, Wiltshire, UK over 50 years. Chapter 3 describes analyses that I have conducted in order to detect changes in fruiting phenology of ten common fungal functional groups extracted from the dataset. Meanwhile, in Chapter 4, host ranged of 8 common fungal genera were explored and responses of mycorrhizas and saprotrophic fungi were compared. Moreover, the question of whether changes in fungal fruiting patterns in the UK could be affected by climatic factors over recording period are discussed in Chapter 5. For spatial aspects of fungal community structure, field studies have been conducted in Chapter 6 and Chapter 7 of the thesis where samples were obtained from study sites in Windsor Forest (Windsor Great Park), Royal Holloway College (Egham, Surrey) and Wivelsfield (West Sussex). Chapter 6 describes experiments on a model species, *Hypholoma fasciculare* to examine whether fruit bodies that fruit in the same place have fruit more than once a year. Chapter 7 contains explanations of an attempt to answer the question whether some individuals have gaps/off-year during their fruiting seasons while there are other individuals belonging to the same species that occur elsewhere. This then followed by identifying factors that could triggers the fruit body formation.

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FFD ……first fruiting date

LFD ……last fruiting date

Chapter 1

General Introduction

Fungi are best known for their role as decomposers, and play a major role in nutrient recycling in ecosystems. Fungi also have direct interactions with plant, animal and bacterial community structure through a wide variety of interactions. Therefore, any interference within fungal community structure may also disrupt the balance of other organisms in the environment. For example, many plants are dependent on mycorrhizal fungi for minerals and nutrients in order to grow. The symbiotic relationship between plant roots and mycorrhizal fungi enables plants to acquire mineral, nutrients and water while fungi obtain sugars in exchange (Peay *et al.* 2008). Absence of appropriate fungi can significantly alter plant community structure (Weber et al. 2005).

Despite our understanding of fungal roles in decomposition activity, nutrient recycling in ecosystems and associations between fungi and other organisms, there are many things relevant to the spatial and temporal aspects of macrofungal communities that have yet to be discovered. The existing studies of fungal community structure have concentrated on several aspects including the diversity and abundance of fruit bodies (Straatsma *et al.* 2001), the importance of exogenous environmental factors in triggering fruit body production (including temperature, rainfall, soil chemical properties, vegetation type, structure and age of the forest stand and host genotype for mycorrhizal species) (e.g. Ruehling & Tyler 1990; Vogt et al. 1981; Last & Fleming 1985), fungal-host associations (e.g. Bruns *et al.* 2002), competition and partitioning of species of various niches (e.g. Bruns 1995). Nevertheless, there are other fascinating spatial and temporal interactions between fungi and other related external environmental factors that still require detailed explanation, such as fruiting phenology, the ability of a species to expand and/or shift their host and also fungal dispersal. Different attempts to measure spatial and temporal variability displayed mixed findings, depending at what scale and aspects the fungal structures being studied. Peay *et al.* (2008) suggested that this may be due to different patterns

between functional groups (e.g. wood decay fungi, soil fungi etc), different taxonomic criteria (e.g. morphology), differences in sampling efficiency (short or long term) (Woodcock *et al.* 2006; Peay *et al.* 2007) and also differences in ecological factors (nutritional mode). Although these differences in pattern usually do not pose a risk of extinction, fungi and their allies may be in jeopardy if habitat size is proven to be one of the causative factors of fungal species richness (Peay *et al.* 2008).

Recent global climate change has been shown to have affected a broad range of organisms with diverse geographical distributions (Ottersen *et al.* 2001; Walther *et al.* 2001; Walther *et al.* 2002). According to Walther *et al.* (2002), these responses, however, do not respond to approximate global averages but instead respond more at a regional scale. In addition, Walther *et al.* (2002) also reported that minimum temperatures that are increasing at twice the rate of maximum temperatures. This results in reduced diurnal temperature ranges and coupled with changes in the rainfall regime, these climatic factors will undoubtedly contribute to heterogeneity in ecological dynamics across systems. Several aspects in ecosystems include the responses seen in phenology, in physiology of organisms, and in the range and distribution of species and the interactions within communities. Phenology is defined by Walther *et al.* (2002) as the timing of seasonal activities for plants and animals in relation to variation in climate and has been suggested to be the most convenient method of examining any changes in the ecology of species in response to climate change. Studies involving various types of taxonomic groups and biological events have demonstrated strong relationships between phenological events and climatic factors, one of which is earlier flowering in many plant species, such as *Betula pubescens, Prunus avium, Sorbus aucuparia* and *Ribes alpinum* in Europe (Chmielewski & Rötzer 2001). Warming in the early spring (February–April) by 1°C causes an advance in flowering of up to 7 days. Besides that, the observed extension of growing season in the study was mainly due to the earlier onset of spring. Furthermore, the effects of climate change on phenology of organisms is also reflected in the long-term analyses by Crick *et al.* (1997) and Sparks (1999) who have discovered earlier nesting and arrival from migration for some bird species. Moreover, earlier breeding were also detected

in several amphibian species in Southern England as reported by Beebee (1995) who have suggested that amphibian reproductive cycles in temperate countries are responding to climate change. Despite advanced development in several organisms, there were also delays and expansion in several phenological events, but these shifts are less pronounced and show more complicated patterns (Walther *et al.* 2002). For example, delays have been found in autumnal leaf colour changes of trees while there was extension in the length of growing season in some areas in Europe (Menzel & Fabian 1999).

Recently, fungal phenology has started to raise attention of several mycologists all over the world. For example, Gange et al. (2007) reported advanced fruiting for autumnal species in England while Kauserud *et al.* (2008,2012) reported delayed fruiting of autumnal species in Norway. On the other hand, advanced fruiting was detected in a 47-year survey of spring-fruiting fungi (Kauserud *et al.* 2009). Recently, Sato *et al.* (2012) have found differences in the fruiting phenology among three common fungal functional groups namely ectomycorrhizal (ECM) fungi, litter decomposers and wood decay fungi. Earlier, Straatsma *et al.* (2001) reported that the peak of mushroom fruiting was around late summer to autumn based on their long-term survey and suggested temperature to be the potential triggering factor. However, all of these studies did not explain trends of fungal fruiting in detail, nor any differences between functional groups across longer time-series.

Climatic factors are thought to be the one of the main drivers of changes in fungal community structure. There is a strong body of literature showing that climate variables such as temperature and rainfall affect temporal patterns of various species of fungi (Zhang *et al.* 2005; Koide *et al.* 2007; Sato *et al.* 2012; A'Bear *et al.* 2013; Jarvis *et al.* 2013). Indeed, it appears that climate is changing globally, and with unpredictable climate at different spatial scales across regions, combined with other potential triggering factors, these could create dynamic fungal assemblages.

Changes in different aspects of fungal community structure over time can result from a variety of factors, either internally or externally. To identify these changes, detailed, long-term data are required to determine trends of fruiting behaviour (e.g. fungal appearance, disappearance and length of fruiting season). Furthermore, long-term studies can also reflected responses of fruiting behaviour to external factors, when combined with time-series data using quantitative statistical methods. For example, Büntgen *et al.* (2012) found a positive correlation between intra-annual autumnal fungal fruiting with regional cumulative rainfall, suggesting increasing fungal fruiting frequency in a year is due to the increasing rate of cumulative of rainfall in late June and early October.

The overall objective of this thesis was to examine some of the spatial and temporal aspects of fungal community structure that are less understood. Such aspects include phenology, fungal-host associations and the relationships between productivity of fruit bodies and weather, which is said to be the main external triggering factor. In addition, I was also interested to determine whether the same individuals are producing fruit bodies at multiple times and also to find out whether species are able to grow at the same place every year.

In *Chapter 3* of this thesis, analysis has been carried out to study fungal fruiting phenology from a 58 y old long term dataset, which was obtained from nearly 1,400 localities within a 30 km radius surrounding the city of Salisbury, UK. Detailed information about the dataset can be referred to *Chapter 2* of the thesis. In total, 368 species were involved in this analysis, which were divided into ten functional groups according to their habitat. Trends for first fruiting date (FFD), last fruiting date (LFD), length of fruiting (RANGE) and average of fruiting date (MEAN) for every species in each functional group were examined across years with regression analysis. I hypothesised that most group may display changes and that there would be variation between groups, in terms of their fruiting patterns. This was followed by examining relationships between these fruiting aspects with the frequency of species in each functional group and also against grand mean fruiting date for all 368 species in the

dataset. For these tests, I hypothesised that there would be significant differences in the frequency of species in each functional group that responded to each of fruiting variables that were examined. Furthermore, in order to obtain a better understanding of responses of fungi at the genus and individual level, several common genera in the dataset that fruit at similar times also were examined. Moreover, these genera were grouped into two categories based on their nutritional mode (mycorrhiza and saprotroph) and patterns between these groups were compared. I hypothesised that mycorrhiza and saprotrophic fungi may show differences in their FFD, LFD, length of fruiting season and also their average fruiting date.

One of the spatial studies in this thesis was examining the possible changes in the associations between fungi and their hosts/substrates. For that, *Chapter 4* of the thesis investigated the fungal-host associations of eight most common genera from the same dataset that was previously used in Chapter 3. Those genera were *Amanita, Boletus, Clitocybe, Collybia, Innocybe, Lactarius, Mycena* and *Russula.* Here, trends in the host range of each species in every genus were compared according to different trophic group; the mycorrhizas and saprotrophs. Changes in fungal host associations, both in terms of extension of host range and the shifting of hosts also were examined. The hypotheses that were made in the beginning of this study were that: 1) there will be differences in the rate of host range expansion and host shift between mycorrhizal and saprotrophic species, and ii) there are tendencies of any species in the dataset to shift host from their common hosts to another. In addition, part of this chapter has been published in Gange *et al.* (2011) in which is an analysis of fungal fruiting of the common fungus *Auricularia auricula-judae*, a species that is often cited as being mostly confined to one host. The records of *A. auricula-judae* were obtained from the same dataset and analysis showed that the host range of this species has changed in the UK over the last 59 y. Besides that, the species has also shown altered phenology, with earlier appearance of fruit bodies and a longer fruiting period, consistent with a response to observed warming trends in climate. Coincidental with the change in fruiting time is an expansion of its host range.

Rainfall and temperature are two environmental factors that are often suggested to be the main triggers of fungal fruit body production. However, to what extent these factors are able to affect the fruiting patterns are still largely unknown. Although, there is no doubt of the effect of these factors on fungal phenology, previous studies did not fully explain the effect of rainfall and temperature on the fruiting pattern of fungal functional groups, genera and groups in different nutritional modes. Therefore, the overall goal of the study in *Chapter 5* was to examine which climatic factors show most influence on the observed variation in the long-term phenology of macrofungi in Chapter 3. Apart from that, I also tested the following hypotheses: i) the relationship between phenology of each functional group and temperature parameters varies year to year and ii) there are differences in climate-induced responses between mycorrhizal and saprotrophic species in the dataset that previously used in Chapter 3 and 4 of the thesis.

The majority of fungi usually appear in the autumn in Britain, although some species may be seen in a different time of year. This is probably due to the rise in temperature during summer which causing the substrates to warm up, together with frequent rainfall that provides warm and a damp environment, that encourage fungi to fruit. Moreover, studies have revealed that several autumnal species tend to be found fruiting twice a year, in spring also (Gange *et al*. 2007). Therefore, *Chapter 6* aimed to determine whether the same individuals are producing fruit bodies multiple times throughout the year or the following year. An inoculation method was used to observe interactions of *Hypholoma fasciculare* in three different study sites ranging from a year to three year observations. I hypothesised that the same individuals will produce fruit bodies more than once throughout the year.

Chapter 7 focuses on studies of seasonal occurrence of 18 common autumnal species recorded in Windsor Great Park in three consecutive years (2010 – 2012). In this study, I hypothesised that some individuals may have gaps/off-year during their fruiting seasons while there are other individuals belonging to the same species that occur elsewhere. This then followed to my next hypothesis that weather would not be the

only factor that triggers the fruit body formation, which suggests that there other factors such as mycelial interactions towards resource availability and gases in atmosphere that encourage mycelia to form primordia. Besides that, the findings of this study were also compared with the previous results in Chapter 6 given that records of fungal species were obtained at the same sites and within the same period of time. I further expected variations in the sequences of fruiting time and frequency of occurrence over years for each species which would likely be due to individualistic responses towards climatic conditions and resource availability.

Chapter 2

Data set properties

The data set used for studies in Chapters 3, 4 and 5 consists of 59,868 records of fruit body individuals, 7,486 more records than the one previously analysed by Gange et al. (2007) with additional records of macrofungi for the period 2005 – 2008. The earliest date where the fruit body was found has been recorded in the year 1937. However, due to the scattered number of records in the earlier records, only those from the year 1950 have been taken into account in the analysis, giving 58 years of recording.

In total, the data set represented 368 species, which were obtained from nearly 1,400 localities within a 30 km radius surrounding the city of Salisbury, Wiltshire, UK which covered approximately 2,828 km^2 of area. The sampling area covered both deciduous and coniferous tree species, mostly dominated by *Quercus robur* (English Oak), *Fagus sylvatica* (Common Beech) and *Betula pendula* (Silver Birch). Sampling sites included most of the natural woodlands and plantations in the New Forest and Salisbury Plain areas. However, a wide variety of other woodlands, and localities such as natural grasslands, pastures, churchyards, waste ground and agricultural land were also included. Every visit to any site is hereafter described as 'foray'.

In terms of sampling methodology, each locality was randomly selected without relying on any systematic basis, in order to avoid bias in results. For each particular visit at every locality, at least three hours were spent as the minimal time for a fungal 'foray'. The foray was held at least once a week of every year and each locality was visited at least once per year. Only fresh fruit bodies were put into the records, excluding the perennial species with permanent fruit body structures. Most fungal species in the data set were collected and identified by Edward G. Gange (EGG). If this was not possible, then identities were confirmed by the Royal Botanic Gardens, Kew.

The data set consists of information on the species entity, date of collection, the collector, host association, localities and grid reference where fungi were collected.

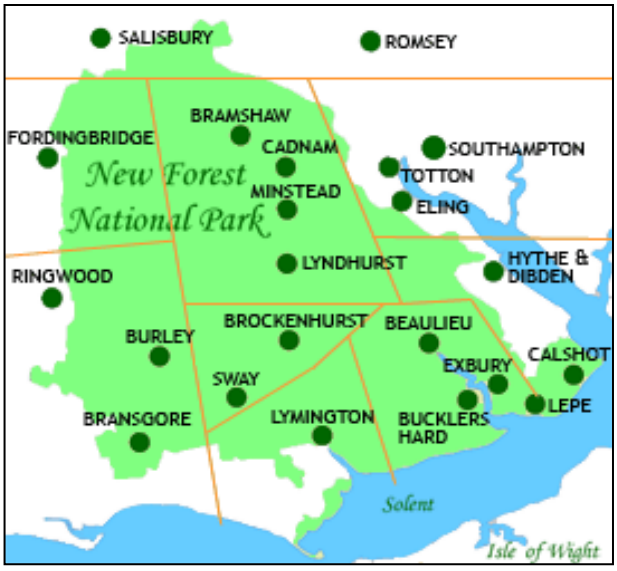


Figure 2.1 Map of study area ranging from New Forest National Park to Salisbury.

Furthermore, standard meteorological data including daily temperature, daily rainfall and relative humidity data during the period of fruit body recording were obtained from two of the nearest local weather stations, which were Hurn Airport (currently known as Bournemouth Airport) (Latitude: 50.78°, Longitude: -1.84°) and Southampton Weather Station (Latitude: 50.9°, Longitude: -1.40°).

With so much fungal information in the original data set, a summary of species was created that contained essential fruiting aspects for each of the fungal species. The aspects included were first fruiting date (FFD), last fruiting date (LFD), length of fruiting period (RANGE), the average date of fruiting each year (MEAN), number of records per year and the ratio of records to foray number for every species in the data set. FFD is defined as the first date in a year when the fresh fruit body was found. Meanwhile, LFD was the last date of the year when the fresh fruit body was seen. The average date of first and last fruiting of each species was calculated for the entire period of study. The range of fruiting season (RANGE) was determined by subtracting an average date of first fruiting from an average date of last fruiting of each species in the data set. The average date of fruiting period of each species in each year was calculated as the mean of all records in any one year for that species across 58 years.

To examine phenological changes, trends for FFD, LFD and RANGE data for each fungal species were examined with multiple regression analysis where the average date of FFD, LFD, and RANGE of each of the species was regressed against years. The conservative method of linear regression was applied to relate mean fruiting date to year, with the number of records for a species in each year used as a weighting factor, to avoid bias from 'bad' fruiting years. Meanwhile, the average date of appearance (mean of all records over 58 years) for every species was calculated and plotted against the regression coefficient which was obtained by relating FFD to year with number of records applied as weighing factor.

All 368 species were divided into ten functional groups: i) grassland (n = 47), ii) mycorrhiza with coniferous trees (n = 12), iii) leaf litter (n = 48), iv) mycorrhiza with deciduous trees (n = 75), v) live leaves (n = 11), vi) needle litter (n = 9), vii) manure (n = 10), viii) soil (n = 14), ix) living trees (n = 15) and x) dead wood (n = 127) to enable comparisons of the responses of all group. A complete list of species used in the analysis is given in the Appendix.

Chapter 3

Changes in fungal fruiting in a 58 year historical data set in southern England

3.1 Introduction

3.1.1 Understanding fungal fruiting phenology

Fungal fruiting phenology is a new field of mycology in which the literature is still lacking and which requires far more comprehensive studies covering various aspects of fruiting. Knowledge of fungal fruiting phenology offers numerous opportunities to improve the understanding of their community structure. The presence of fruit bodies is indicative of the presence of the species in the substrate, though of course the opposite is not always true (Gardes & Bruns 1996). Therefore an understanding of this field will be able to support the analysis of observation e.g. by knowing how likely a species is to be seen in a particular condition, we will be able to predict its presence or absence at sites (Mackenzie &Royle 2005; Newbound *et al*. 2010). Also, knowledge of fungal fruiting phenology is important to guide the design of fruit body surveys and a way to explain their findings (Newbound *et al.* 2010). If the causes of fungal fruiting are known, the timing and intensity of surveys can be planned (Newbound *et al.* 2010). Fruit body surveys are a basis for documenting fungal diversity, as sporocarps can be identified to the species level and having these recorded in a good systematic system/database can provide an insight into the characteristics of fungi and may explain their relationship/associations with their non-living environment. Apart from that, due to the important associations between fungal community structure and their environmental conditions which may involve physical, chemical or biotic factors, the effects of any changing environmental factors on fungal fruiting patterns can be predicted. Fungi play an important role in ecosystem functioning especially in the decomposition of organic matter and nutrient cycling in the soil. Therefore, any

changes in fungal fruiting could reflect changes in mycelial growth and potentially affect the ecosystem services of the soil biota.

3.1.2 Factors that contribute to the production of fruit bodies

Many field studies have shown that there are a number of environmental factors contributing to the production of fruit bodies and the trigging of the primordial formation of macrofungi in the natural environment. Some have shown that the productivity of above-ground fruit bodies is related to annual climate conditions i.e. average monthly rainfall and average monthly temperature (e.g. Lagana *et al.* 2002; Salerni *et al.* 2002; de Aragón *et al.* 2007; Krebs *et al.* 2008; Pinna *et al*. 2010). Regarding rainfall and temperature, a few attempts to explain the duration of fungal fruiting in relation to climate change have e recently been discussed (Straatsma *et al*. 2001; Mihail *et al.* 2007; Gange *et al*. 2007; Kauserud *et al*. 2008, 2012).

Furthermore, the productivity of fungi is also determined by habitat characteristics. Generally, forest stands display greater epigeous mushroom productivity than mature stands (Pinna *et al*. 2010). Neville *et al*. (2002) revealed that there were significant associations between soil depth and type of mycorrhizal association in aspen, supporting the hypothesis that ectomycorrhizal levels were highest in the shallow organic layer and arbuscular mycorrhizal levels were highest in the deeper mineral soil.

The plant host has been identified as an influential factor in the production of fruit bodies, especially for ectomycorrhizal species, due to the need for some nutritional elements to build sporophores in the forest (Selosse *et al.* 2001; Dickie *et al*. 2010). However, this factor is considered as an indirect effect and through the differences of leaf fall quality in several host species, there may be key changes in the litter and topsoil chemical composition that in turn, may affect the ECM community assemblage (Aponte *et al*. 2010).

3.1.3 The use of historical data in order to determine fungal fruiting pattern in a long-term basis

A complete and understandable data set is a necessary tool for documenting every single fruit body found in the field. Even though the records of fungi only partially represent the fungi in the ecosystem, however, with proper, systematic methods of analysing the data, the overall summary for the observed aspects can be achieved. Elaborate and long-term data sets are required to summarise the occurrence and the behaviour of fruit bodies which are mostly affected by environmental conditions, such as temperature and precipitation (Straatsma *et al.* 2001). Many surveys have been conducted to look for productivity of fruit bodies (e.g. Wasterlund & Ingelog 1981; Last & Fleming 1985; de Aragón 2007) fungal diversity (e.g Vogt *et al*. 1992; Watling 1995; Schmit *et al*. 1999; Straatsma *et al.* 2001; Richard *et al.* 2004; Baptista *et al*. 2010;) and substrate preference of the macrofungi (e.g. Gange *et al*. 2011; Martínez-García & Pugnaire 2011). However a study of the dates or the length of fruiting period on a long-term basis is still lacking. By using long-term data to detect any changes in fungal fruiting patterns, it allows for a comparison of current and historical data of fruiting bodies, constituting a valuable tool for management and conservation strategies (Molina *et al*. 2001; Richard *et al*. 2004). Most studies on the duration of fungal fruiting have been performed on a short-term basis ranging from one year to 8 years of data collection (Vogt *et al*. 1992; Mihail *et al*. 2007; Baptista *et al.* 2010; Pinna *et al.* 2010). For some purposes, one year of sampling is enough however most of the research questions may need longer periods of investigation (Vogt *et al*. 1992). Therefore, the present study was carried out to: i) analyse trends for first fruiting date (FFD), last fruiting date (LFD), length of fruiting (RANGE) and average of fruiting date (MEAN) for every species in different functional groups from a 58 y long-term dataset, ii) examine relationships between these fruiting aspects with the frequency of species in each functional group and iii) examine common genera in the dataset that fruit at similar times.

3.2 Methods and Analysis

3.2.1 Data Collection

The data set used for the study is the one previously analysed by Gange *et al.* (2007) with additional records of macrofungi for the period 2005-2008.

If not otherwise stated in Chapter 2, all analyses were carried out with the following methodology.

3.2.2 Analyses

Regression coefficients of FFD, LFD, RANGE and MEAN of every species in each group were plotted against frequency of species recorded in each ecological group to allow comparisons between number of species that appear early or later in the fruiting season. A positive regression value indicates that a species shows delay in fruiting aspect meanwhile a negative represents earlier fruiting. Species used in these analyses were those that were represented by at least 20 years' worth of records. All statistical analyses were conducted with the UNISTAT 4.53 Software Package.

Further analysis was conducted to examine the relationship between each fruiting aspect (FFD, LFD, RANGE and MEAN) and mean fruiting date (MFD) for each of the species in the data set. Furthermore, analysis of responses of species within genera that fruit at similar times also were conducted on several common genera in the data set which included the genera *Amanita*, *Inocybe*, *Lactarius*, *Russula*, *Clitocybe*, *Collybia*, and *Mycena,* to obtain a better understanding of the fruiting aspects of individual species.

3.3 Results

3.3.1 Changes of first fruiting date, last fruiting date, length of fruiting and average of fruiting of each ecological groups

Most ecological groups have shown changes in their fruiting aspects throughout 58 years of data collection (Figure 3.1). However, the proportions of species that show changes in the four fruiting aspects were different from one functional group to another. Of the four aspects analysed, the length of fruiting (RANGE) has shown considerably higher proportions of significant changes in most groups especially for fungi inhabiting grass, leaf litter, needle litter, manure, living trees, dead wood and mycorrhizal fungi in both coniferous and deciduous trees. Meanwhile, for first fruiting date, it can be seen that proportions of species that show significant changes were around 40% to 90% of the total species in the ten groups studied. Fungi inhabiting live leaves have shown the highest proportion of species showing earlier appearance (91%) (Figure 3.1e) meanwhile fungi remained on manure show the lowest (40%) (Figure 3.1g). On the other hand, the last fruiting dates for half of the total species in all ecological groups also have undergone changes. The greater rate of change was detected in soil fungi where 93% of their total species have experienced changes in their last fruiting date (LFD) (Figure 3.1h). In other respects, the average date of fruiting was also different between groups. 82% of fungal species found inhabiting live leaves have shown changes of their mean date, while needle litter species have shown few responses in mean date, with only one species showing a significant change (Figure 3.1f).

3.3.2 Frequency of species vs. regression coefficient of first fruiting date (FFD)

A wide range of responses in FFD of species was found in all groups ranging from positive to negative values of regression coefficients (Figure 3.2a-j). Groups with higher number of species display a big range of values e.g. the wood-decayers (Figure 3.2j) whilst the groups with smaller number of species tend to have narrow ranges e.g. fungi

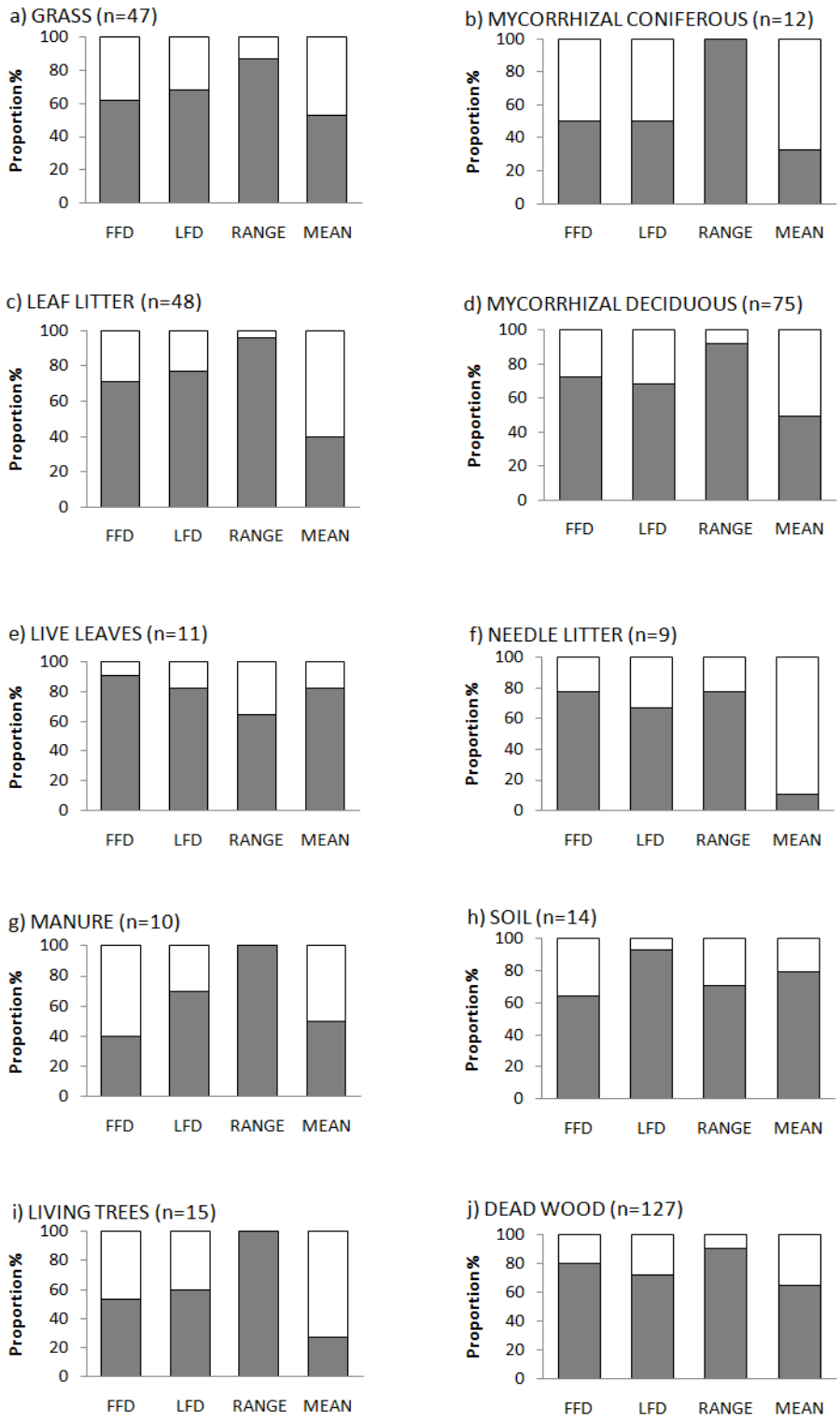


Figure 3.1(a-j) Proportion of species showing significant changes in first fruiting date (FFD), last fruiting date (LFD), length of fruiting (RANGE) and average of fruiting (MEAN) for different ecological groups. Dark-coloured bars indicate significant changes in species proportion for each fruiting parameters meanwhile light-coloured bars showing non-significant changes in species proportion for each fruiting parameters.

inhabiting needle litter (Figure 3.2f). Some groups showed mostly positive (delayed) responses such as needle litter dwellers (Figure 3.2f). In some groups most values were positive, i.e. delayed appearance, e.g. soil fungi (Figure 3.2h). However, most of the groups displayed negative regressions meaning earlier appearance in the season. Among these earlier fruiters, some have shown much greater responses than others e.g. fungi inhabiting live leaves (Figure 3.2e). On the whole, the vast majority of the bars that show the changes in species were found in the negative range of regression coefficient of FFD, indicating that most species in all groups tend to have earlier appearance during the fruiting season. Meanwhile, individualistic responses were common as not every species showed significant results. However, there were groups which have shown clear patterns, such as wood decayers, in which most coefficients were negative. This group formed the highest number of species and majority of them have shown earlier appearance over the 58 years.

3.3.3 Frequency of species vs. regression coefficient of last fruiting date (LFD)

In contrast to FFD, the LFD of most species in all groups have shown changes wherein their disappearance has become later (Figure 3.3a-j). Of all later fruiters, fungi found on grass have shown a wider range of regression coefficients compared to the other groups (Figure 3.3a). Surprisingly, there were groups which have an early FFD and subsequently tend to have later LFD. Those inhabiting leaf litter under deciduous trees (Figure 3.3c) and fungi inhabiting living trees (Figure 3.3i) had FFDs that were earlier, but also also displayed later disappearance.

3.3.4 Frequency of species vs. regression coefficient of length of fruiting season (Range)

Interestingly, all ecological groups have shown similar patterns where most species were found at the positive range of regression coefficient indicating that they tend to have an extended length of fruiting (Figure 3.4a-j). Meanwhile, the individualistic responses of certain groups were again common, and likely restricted to individual's

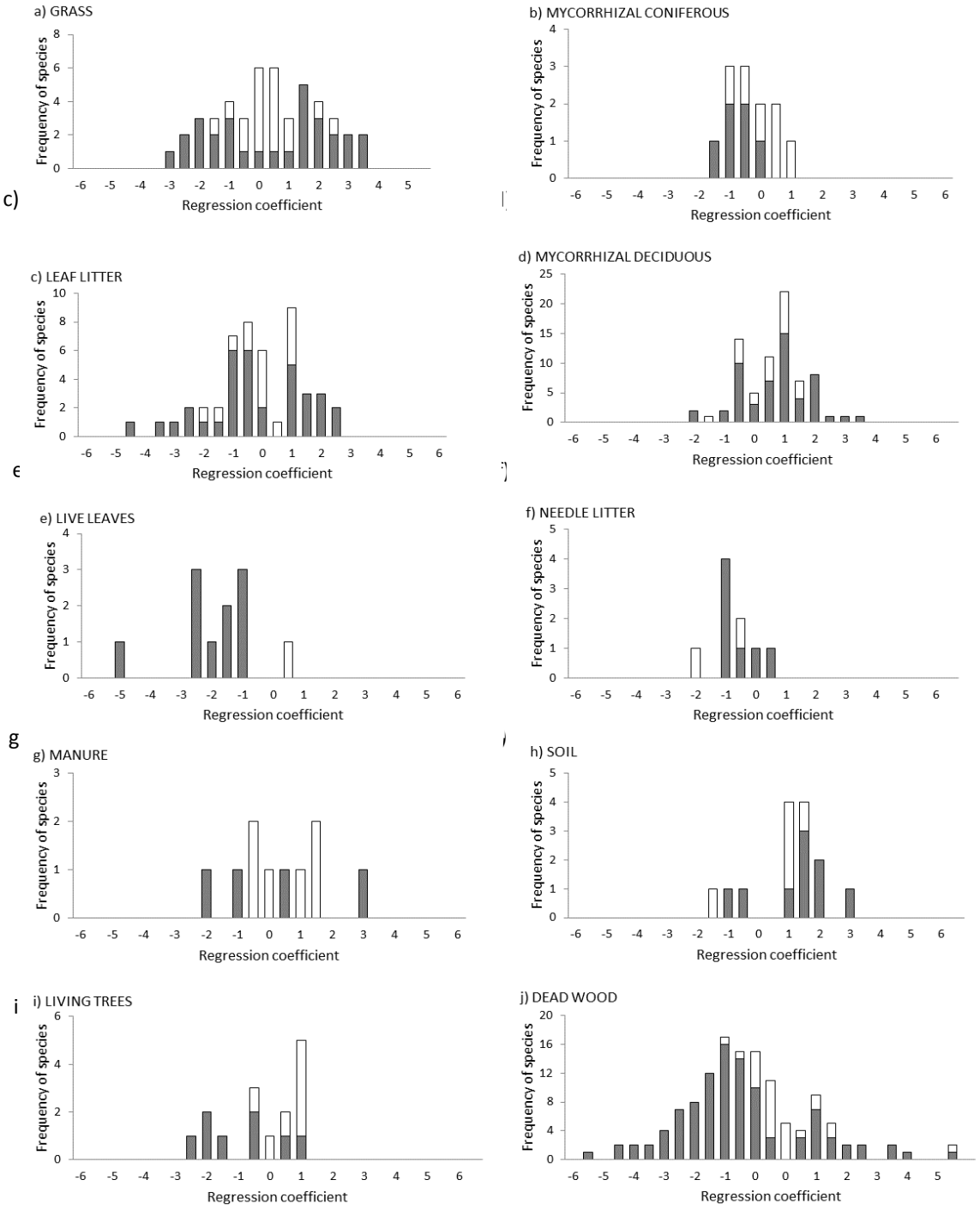


Figure 3.2(a-j) Frequency of species against regression coefficient of first fruiting date (FFD). Dark-coloured bars indicate number of species which displayed significant changes in their FFD. White-coloured bars indicate number of species showing unchanged FFD.

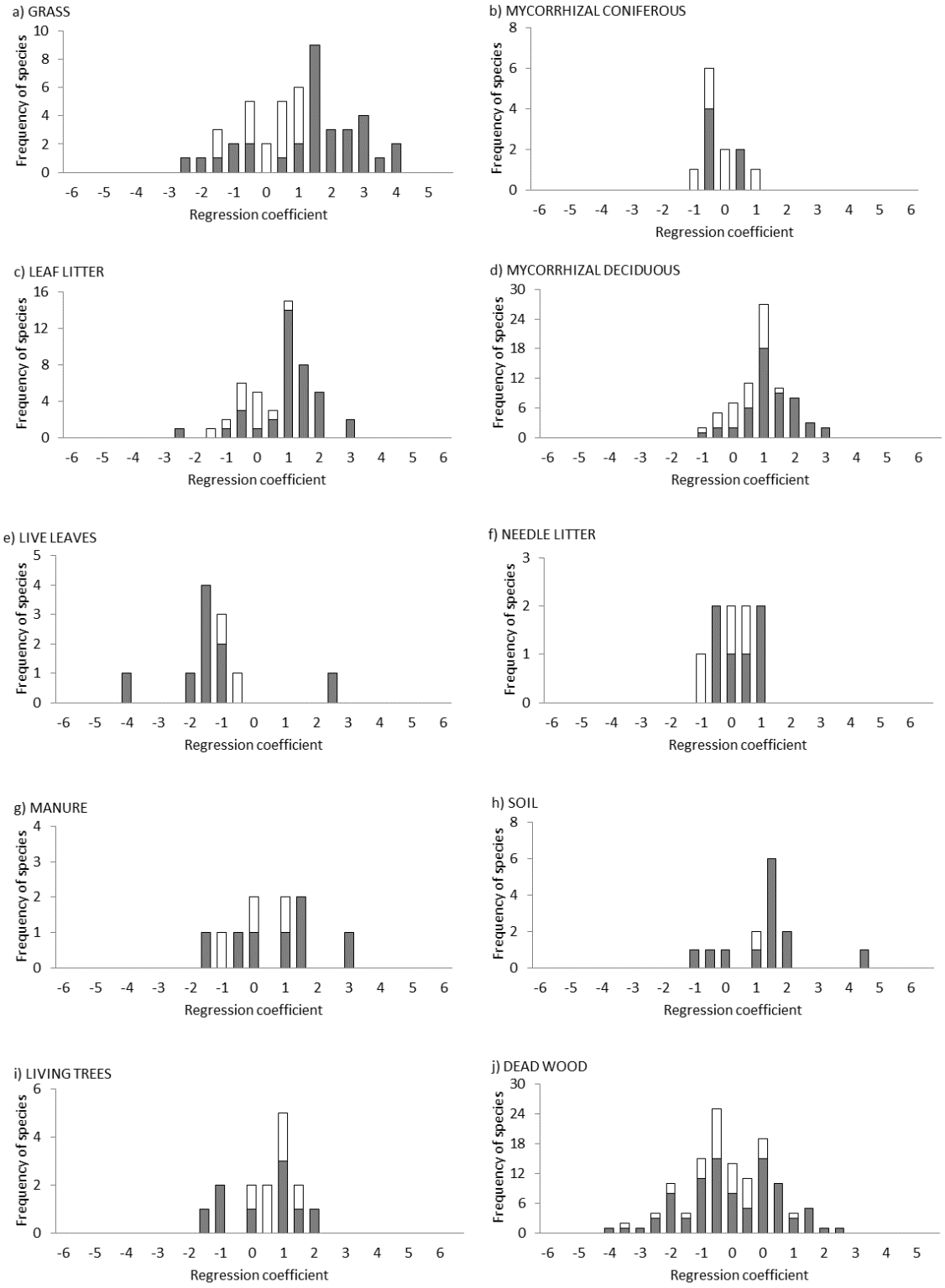


Figure 3.3(a-j) Frequency of species against regression coefficient of last fruiting date (LFD). Dark-coloured bars indicate number of species which displayed significant changes in their LFD. White-coloured bars indicate number of species showing unchanged LFD.

behaviour especially for all species found in manure (Figure 3.4g), living trees (Figure 3.4i) and mycorrhizal under coniferous trees (Figure 3.4b).

3.3.5 Frequency of species vs. regression coefficient of MEAN

Various trends were seen across different functional groups where some species tend to have earlier average fruiting dates and some have delayed fruiting. Most species found on grass, mycorrhizal fungi found in deciduous trees and soil fungi have become later whereas the majority of fungi inhabiting live leaves, wood-decay fungi and mycorrhizal in coniferous trees show earlier averages (Figure 3.5).

3.3.6 Relationship between regression coefficients of first fruiting date (FFD) versus year and overall mean fruiting date (MFD)

For all groups, there was a tendency for early fruiters to show delays in appearance, while later species showed advances (Figure 3.6). Negative relations between MFD and regression coefficient of FFD were seen in three ecological groups; mycorrhizal with deciduous trees (Figure 3.6d), fungi inhabiting needle litter (Figure 3.6f) and wood-decay fungi (Figure 3.6j). This suggests that late fruiters tend to have an advanced appearance, while early fruiters have delayed appearance.

3.3.7 Relationship between regression coefficient of last fruiting date (LFD) and mean fruiting date (MFD)

With LFD, most groups displayed no trend, and in only one (deciduous mycorrhizas) was this significant in the relationship between regression coefficient of LFD and MFD (Figure 3.7). This negative relation indicates that later fruiters tend to disappear earlier than species that fruit earlier in the season.

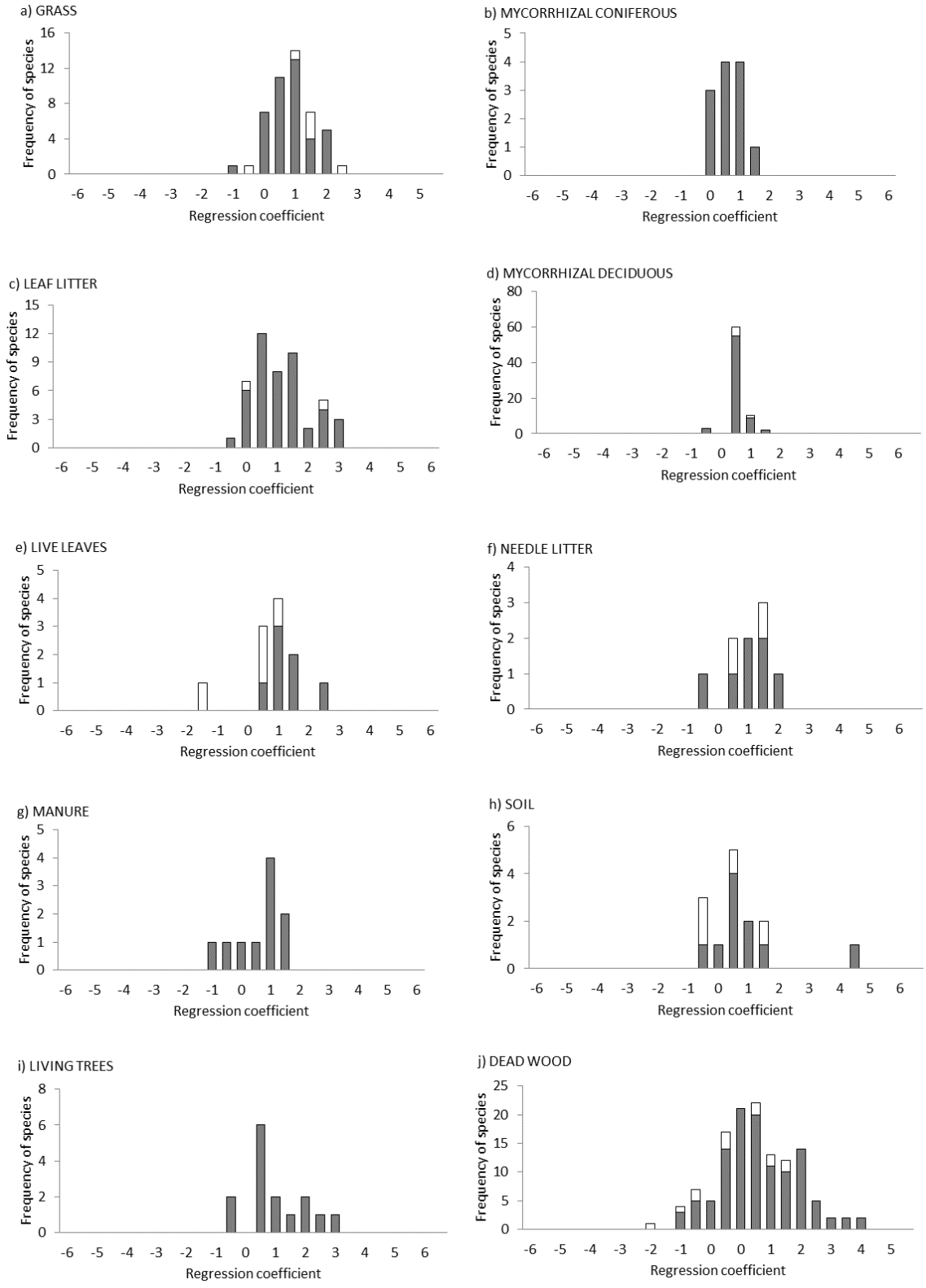


Figure 3.4(a-j) Frequency of species against regression coefficient of length of fruiting (RANGE). Dark-coloured bars indicate number of species which displayed significant changes in their RANGE. White-coloured bars indicate number of species showing unchanged RANGE.

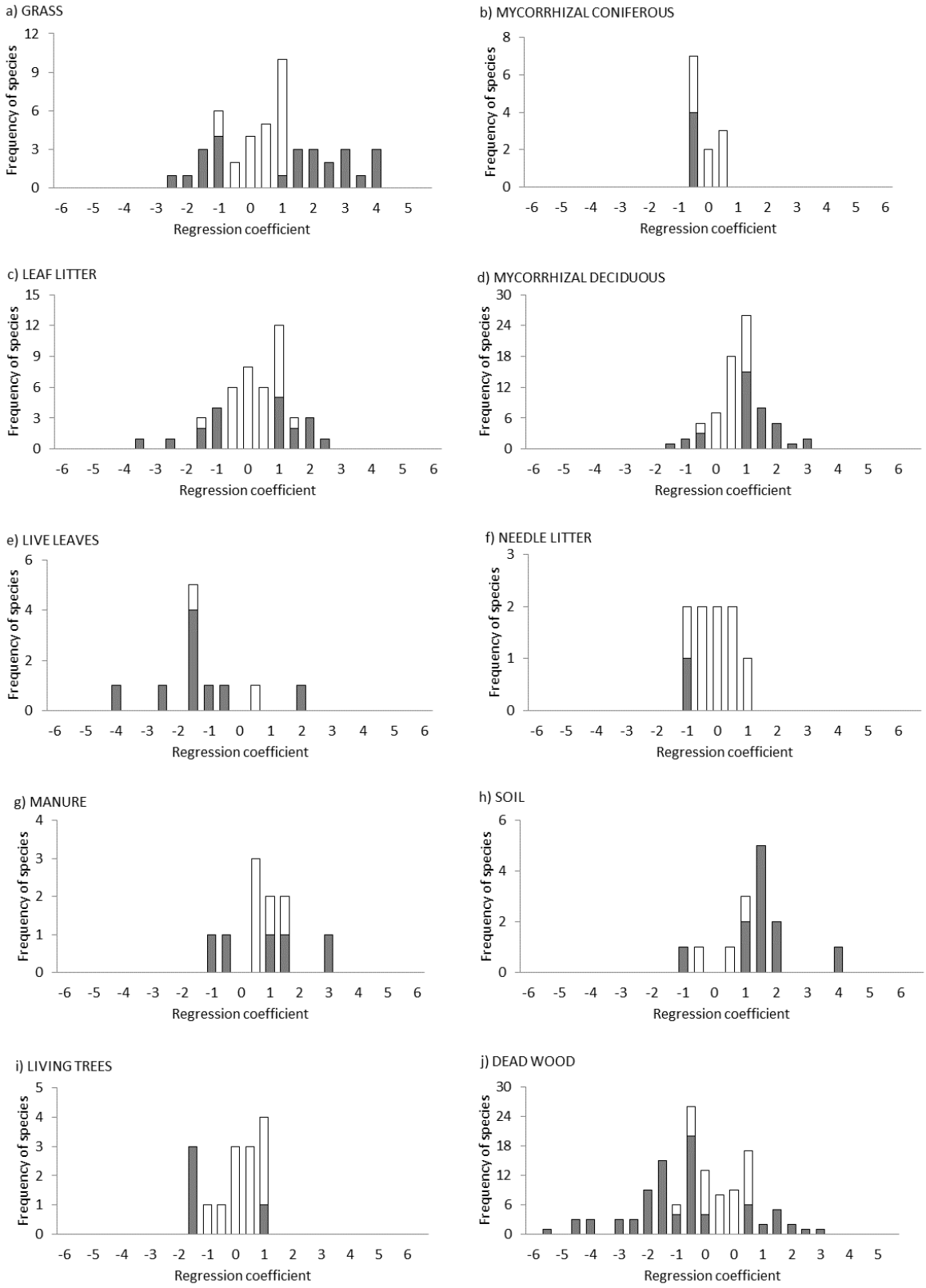


Figure 3.5(a-j) Frequency of species against regression coefficient of average of fruiting (MEAN). Dark-coloured bars indicate number of species which displayed significant changes in their MEAN. White-coloured bars indicate number of species showing unchanged MEAN.

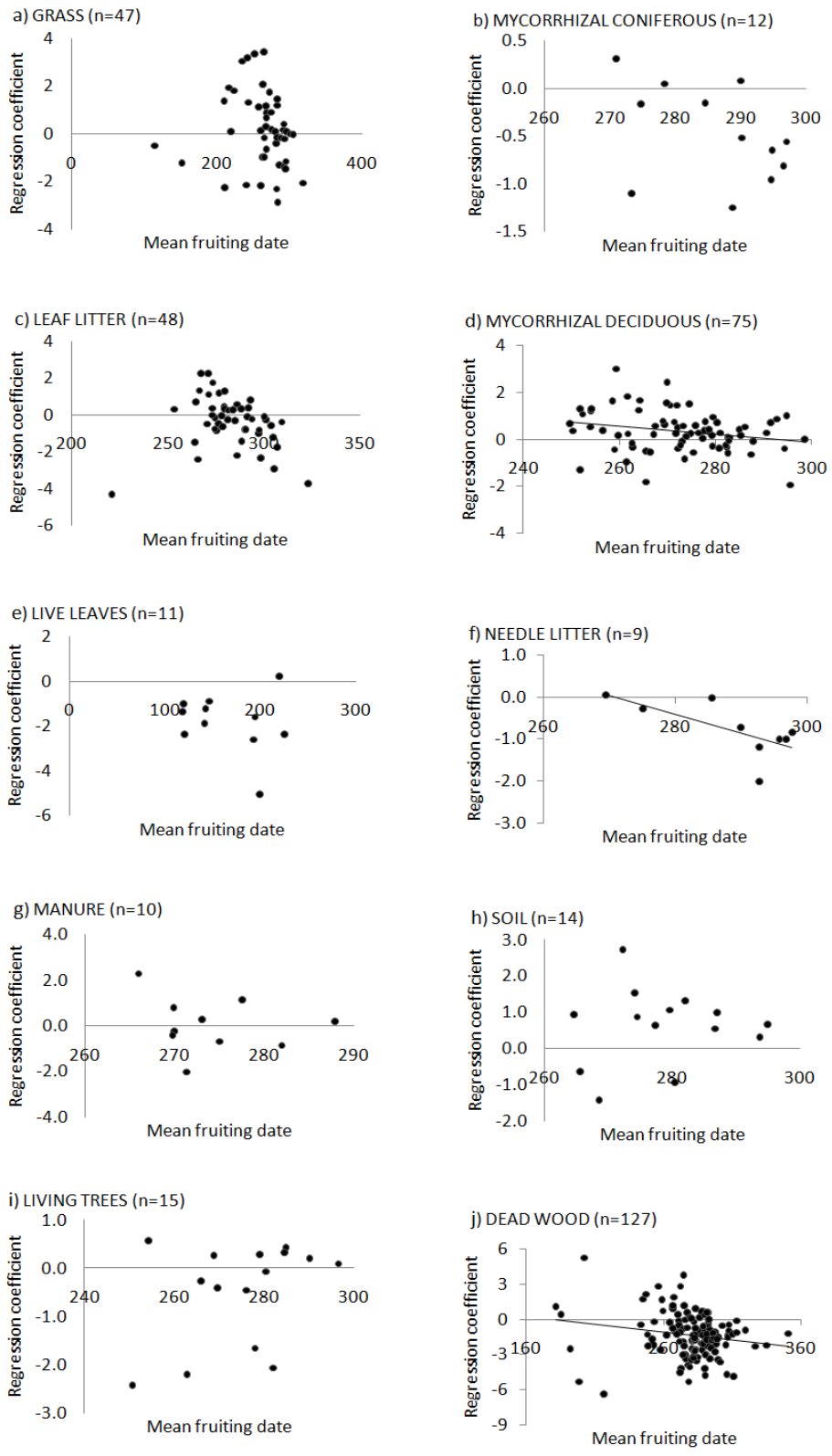


Figure 3.6(a-j) Relationship between regression coefficients of first fruiting date (FFD) vs. year and mean fruiting date (MFD). Significant relations indicated by linear lines.

3.3.8 Relationship between regression coefficient of length of fruiting (RANGE) and mean fruiting date (MFD)

Most groups showed positive coefficients, indicating range expansion, but there was very little evidence that early or later fruiters showed different responses (Figure 3.8). In only one group (needle litter fungi) was a positive relation found, indicating that the later a species appeared, the greater the expansion in its range (Figure 3.8f).

3.3.9 Relationship between regression coefficients of average of fruiting (MEAN) and mean fruiting date (MFD)

There was a tendency for early fruiters to have delays in their average of fruiting, while later species showed advances (Figure 3.9). However, significant relationships between MFD and the coefficient of average of fruiting were only seen in two ecological groups; fungi inhabiting needle litter (Figure 3.9f) and wood-decay fungi (Figure 3.9j).

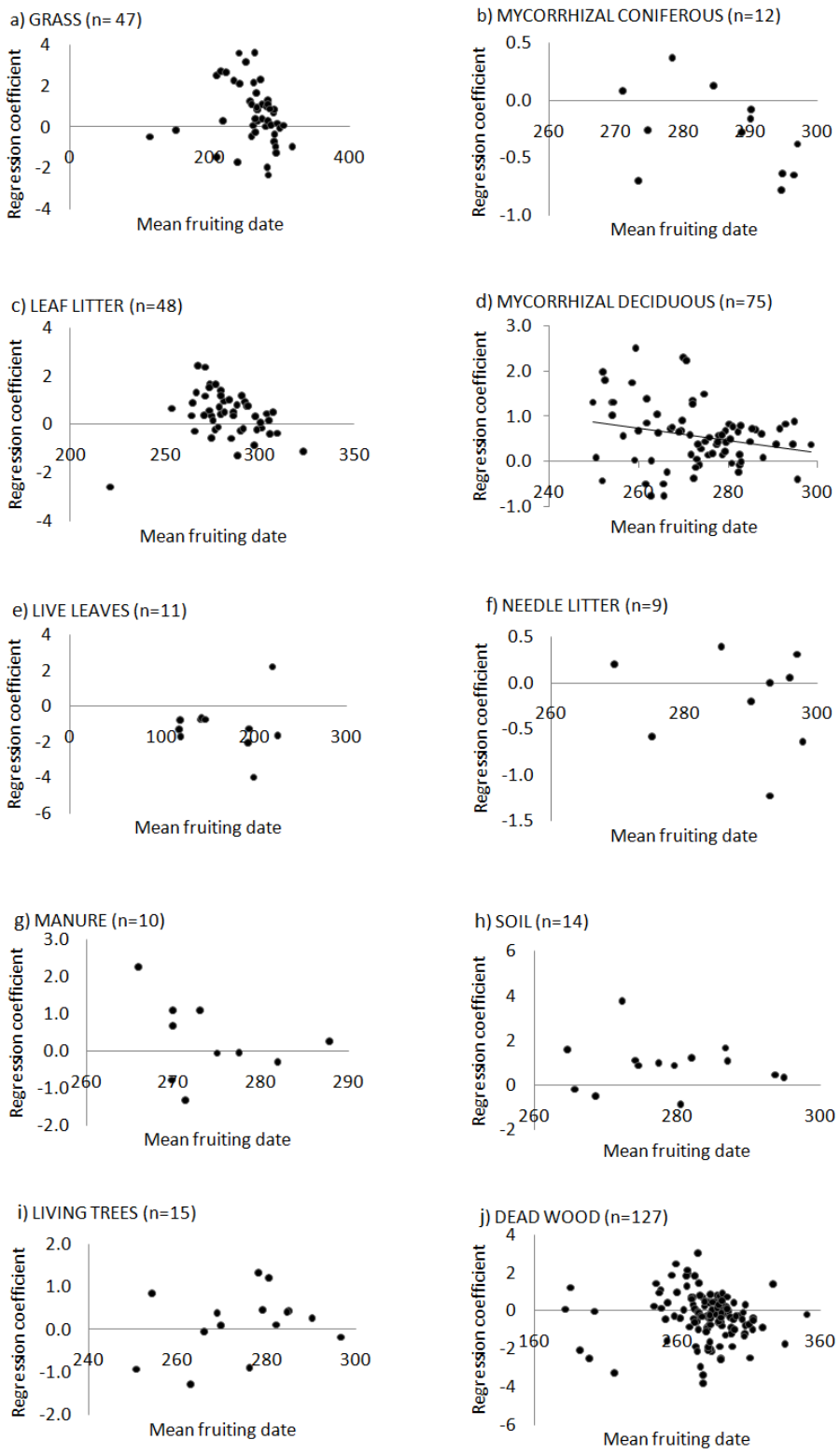


Figure 3.7(a-j) Relationship between regression coefficients of last fruiting date (LFD) vs. year and mean fruiting date (MFD). Significant relations indicated by linear lines.

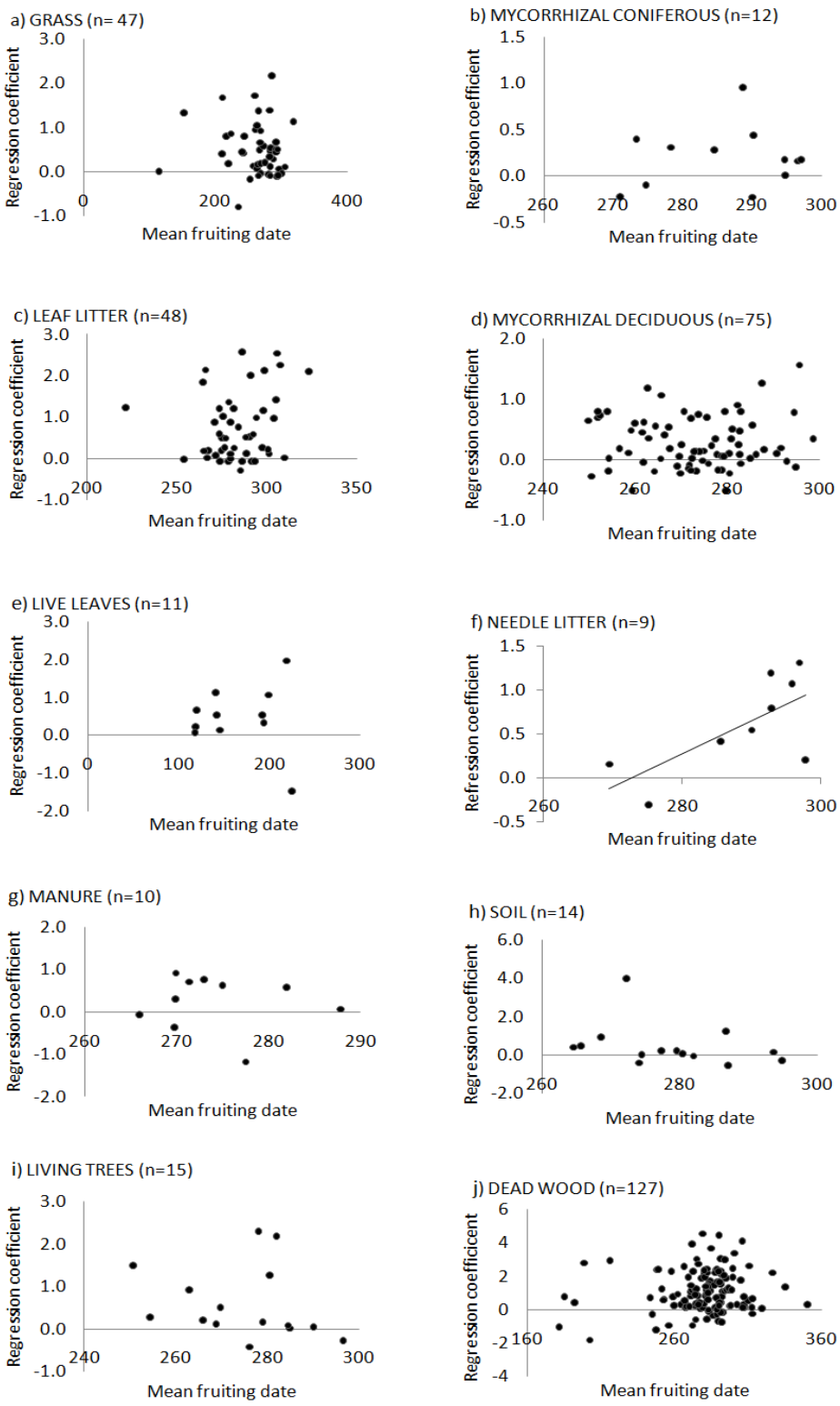


Figure 3.8(a-j) Relationship between regression coefficient of length of fruiting (RANGE) vs. year and mean fruiting date (MFD). Significant relations indicated by linear lines.

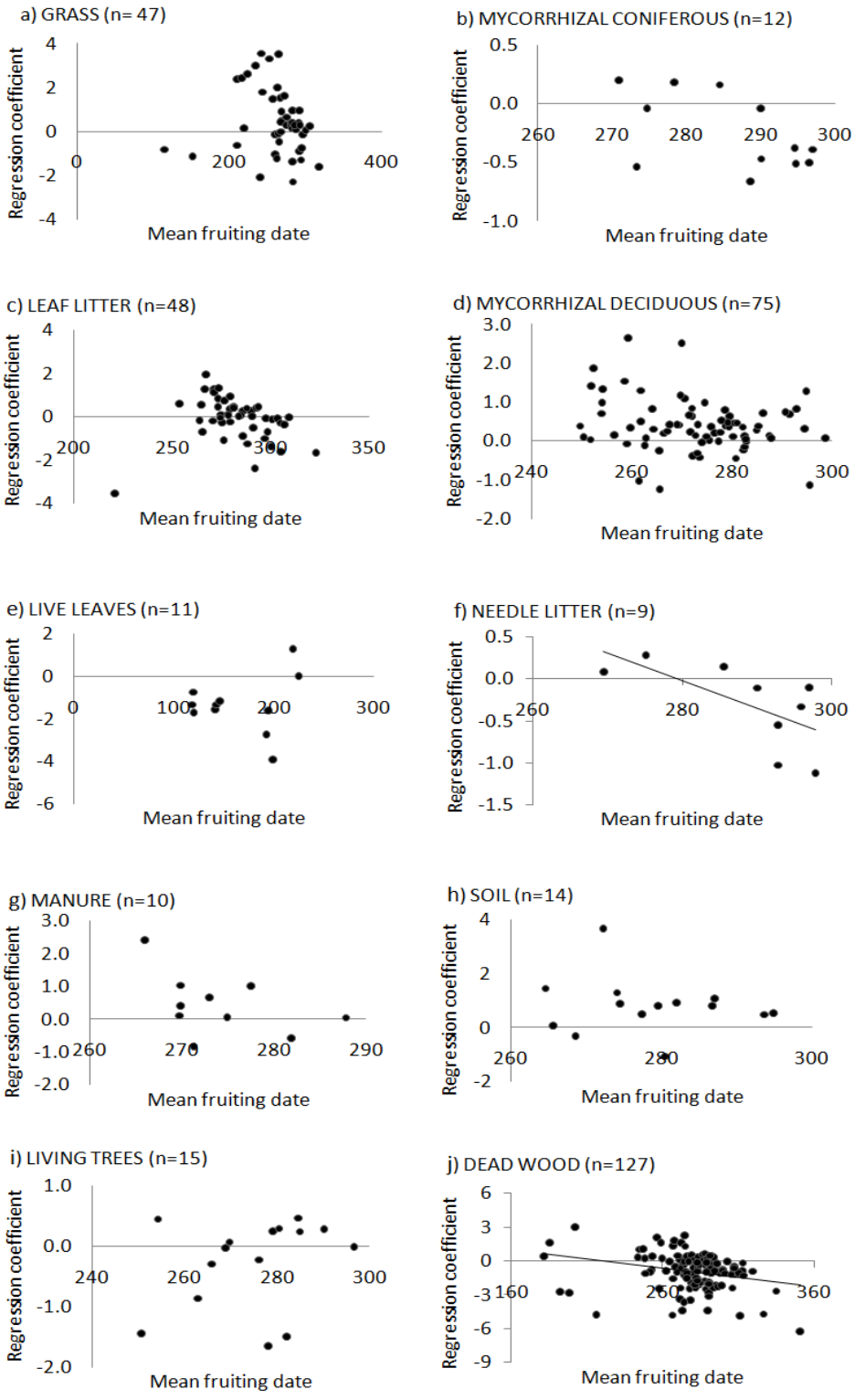


Figure 3.9(a-j) Relationship between regression coefficient of average of fruiting (MEAN) vs. year and mean fruiting date (MFD). Significant relations indicated by linear lines.

3.3.10 Responses of genera that fruit at similar times

a) Mycorrhizal genera

Genus *Amanita*

In general, the pattern of change in *Amanita* was not the same for each parameter. It can be seen in Figure 3.10 that most *Amanita* species have shown a trend to early appearance, with five species displaying significant changes in their FFD. There were only two species that showed delays, which were *A. citrina* and *A. muscaria* (Figure 3.10a).

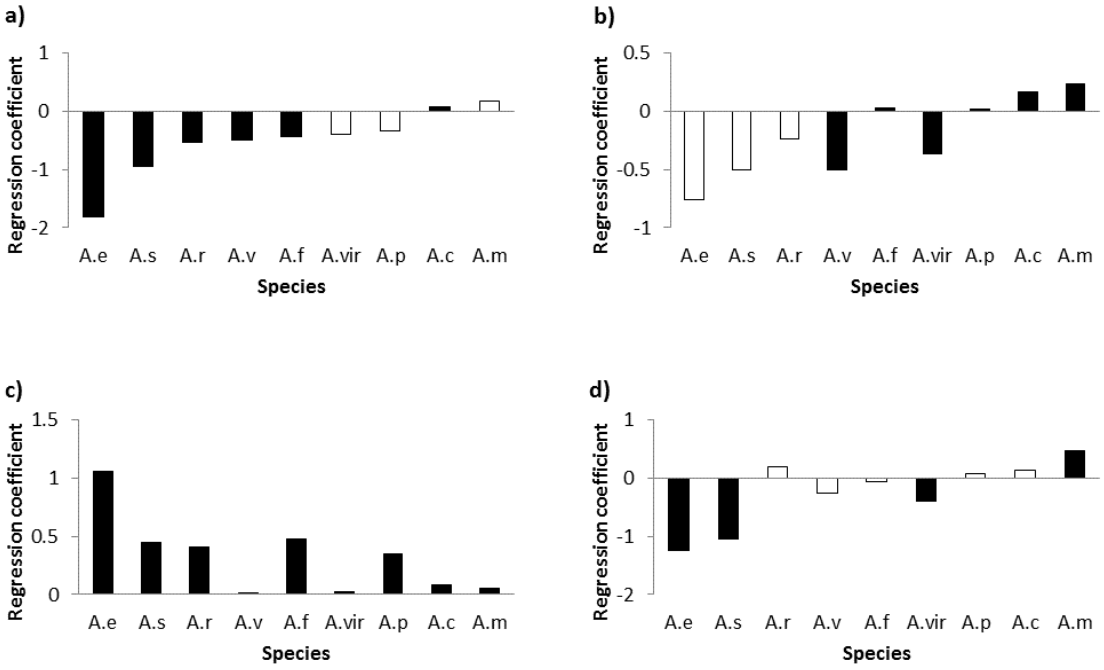


Figure 3.10 The change in a) first fruiting date, b) last fruiting date, c) length of fruiting date and d) average of fruiting date for 9 species of mycorrhizal *Amanita* over 57 years growing under deciduous trees. A.e represents *Amanita echinocephala*; A.s, *A. strobiliformis*; A.r, *A. rubescen*; A.v, *A. vaginata*; A.f, *A. fulva*; A.vir, *A. virosa*; A.p, *A. pantherina*; A.c, *A. citrina*; and A.M, *A. muscaria*. Black-coloured bars indicate species which displayed significant changes meanwhile white-coloured bars indicate species with non-significant changes in each of their fruiting aspects.

Meanwhile four species showed delays in their last fruiting date, whereas five species showed trends to earlier disappearance. Interestingly, all species with delayed LFD have shown significant changes (Figure 3.10b). In terms of their length of fruiting, every species in the genus has shown significant changes with an extension of the fruiting season, but some species have shown a much greater variation in the response than others. The species which had the greatest extension in the fruiting season was *A. echinocephala*, meanwhile the species with the shortest expansion was *A. vaginata* (Figure 3.10c). For the average date of fruiting, *A. echinocephala* and *A. strobiliformis* were two of the species with advanced fruiting compared with other *Amanita* species. In contrast, *A. muscaria* which is the species with the most delayed average date of fruiting, also was found to have significant change in its average of fruiting date, this becoming later (Figure 3.10d).

Genus *Inocybe*

The mycorrhizal *Inocybe* species showed a consistent response in their first fruiting date, with all ten species showing later appearance. The species showing the greatest change in first fruiting date was *I. umbrina* while the species showing the least extension on its first fruit date was *I. asterospora*. It can be seen that all *Inocybe* displayed significant changes in their FFD except *I. patouillardii* (Figure 3.11a). A similar pattern was seen in last fruiting date, where all species showed a delayed fruiting with seven species displayed greater delay in their disappearance. Furthermore, all *Inocybe* species were found to have significant changes in their LFD (Figure 3.11b).

In terms of length of fruiting season, six species showed an extension of the season with *I. patouillardii* exhibiting the greatest extension. Meanwhile, there were four species showed a contraction of the fruiting season with *I. umbrina* having the greatest contraction. Also, it can be seen that species which displayed greater expansion and contraction in their fruiting seasons were found to have significant changes in their fruiting season (Figure 3.11c). All species have shown significant changes in their average date of fruiting except *I. rimosa.* The two species which displayed the most delayed fruiting were *I. umbrina* followed by *I. lacera* (Figure 3.11d).

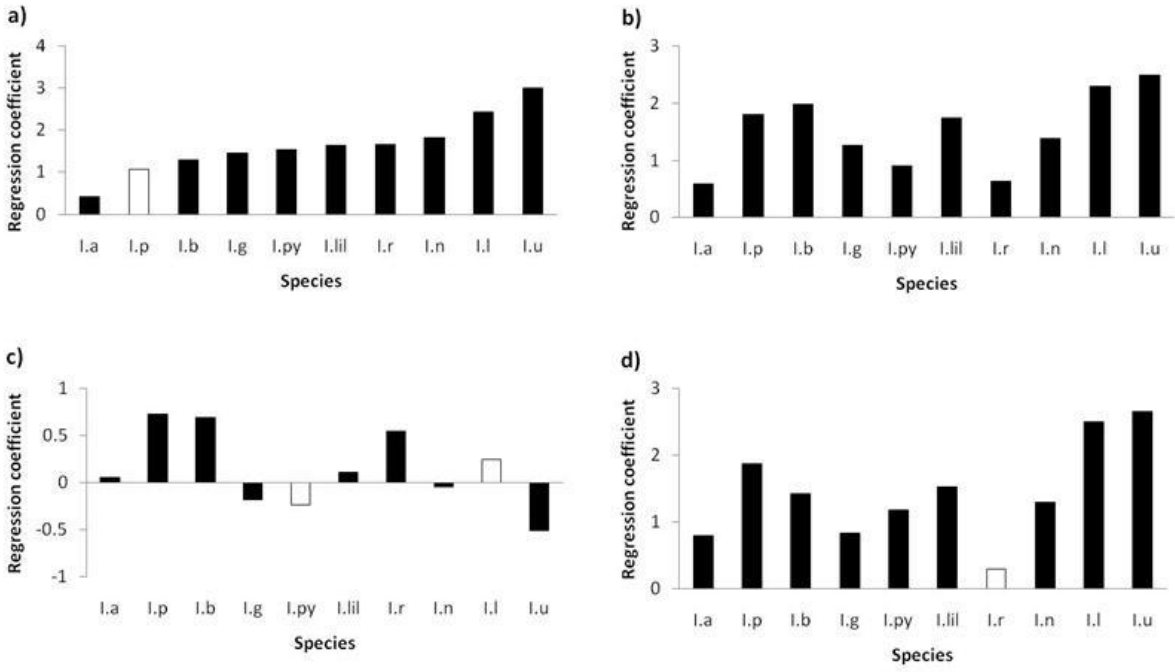


Figure 3.11 The change in a) first fruiting date, b) last fruiting date, c) length of fruiting date and d) average of fruiting date for 10 species of mycorrhizal *Inocybe* over 57 years growing under deciduous trees. I.a represents *Inocybe asterospora*; I.p, *Inocybe patouillardii*; I.b, *I. bongardii*; I.g, *I. geophylla*; I.py, *I. pyriodora*; I.lil, *I. lilacina*; I.r, *I. rimosa*; I.n, *I. nappies*; I.l, *I. lacera*; and I.u, *I. umbrina*. Black-coloured bars indicate species which displayed significant changes meanwhile white-coloured bars indicate species with non-significant changes in each of their fruiting aspects.

Genus *Lactarius*

Response was varied in the first fruiting date for *Lactarius* species. Eleven species showed a delay in their appearance and four species showed earlier appearance in the fruiting season. *L. deliciosus* is one of the early fruiters and it showed the greatest advance in first fruiting date. Also, *L. pyrogalus,* the species with greatest delayed FFD has shown significant change too (Figure 3.12a). Meanwhile, thirteen species showed a delay in their last fruiting date, while only two species were earlier in their last fruiting date. Moreover, all species have shown significant changes in their fruiting season with *L. subdulcis* showing the greatest extension of the fruiting followed by *L. tabidus* and *L. fuliginosus* (Figure 3.12c). Meanwhile, the species with the greatest contraction of the fruiting season was *L. turpis* followed by *L.rufus* and *L. blennius*. Pursuing this further, five species of *Lactarius* have displayed significant changes in their average of fruiting

date shown by their greater delays compared to other species. Those were *L. tabidus*, *L. blennius*, *L. glyciosmus*, *L. turpis* and *L. pyrogalus* (Figure 3.12d).

Genus *Russula*

Figure 3.13a shows that most *Russula* species tend to show delays in their first fruiting date with 79% of species exhibiting a positive regression coefficient value. Moreover, most *Russula* have shown significant changes in their FFD except two species which were *R. heterophylla* and *R. claroflava.* The species with the greatest delay in its appearance was *R. betularum* followed by *R. lepida*. There are only four species that have appeared earlier in the fruiting season; *R. sardonia, R. adusta, R. ochroleuca* and *R. emetica* with *R. sardonia* ahead from the others in its first day of fruiting. Moreover, some species have been delayed even further in their last fruiting date besides their late appearance e.g. *R. cyanoxantha*, *R. heterophylla*, *R. mairei* and *R. fragilis* (Figure 3.13b). Several species have shown interesting changes in their first and last fruiting, where species such as *R. ochroleuca* had an earlier appearance in its first fruiting but seem to be delayed in its last fruiting date. This led to a considerable extension of its season. Not only have that, all *Russula* shown significant changes in their length of fruiting season (Figure 3.13c). There were four species with greater delay in response to the changes in average of fruiting led by *R. lepida*, followed by *R. betularum, R. aeruginea* and *R. delica*. These species were among the species that showed greater delay on the first day they were found and also on the last day they were seen (Figure 3.13d).

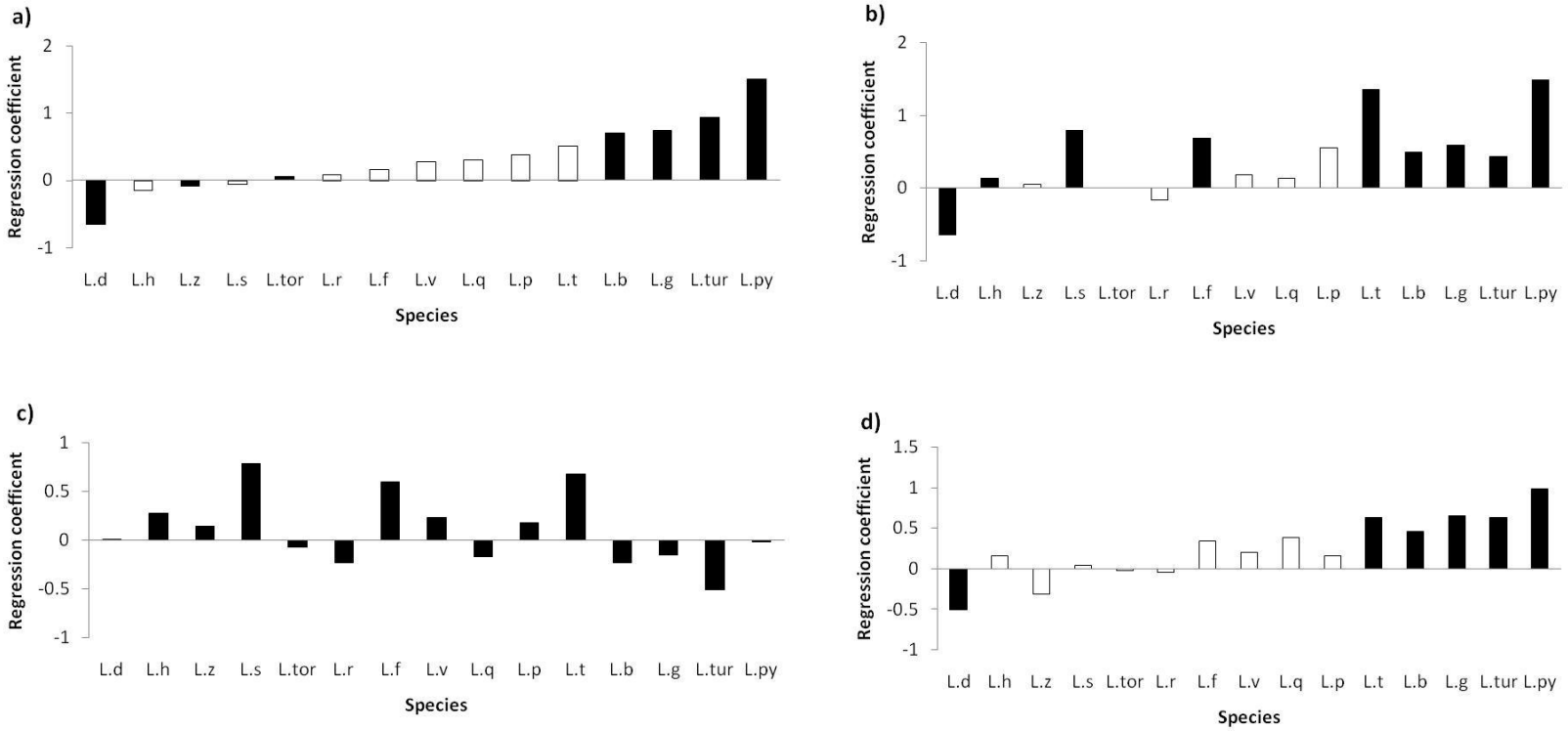


Figure 3.12 The change in a) first fruiting date, b) last fruiting date, c) length of fruiting date and d) average of fruiting date for 15 species of mycorrhizal *Lactarius* over 57 years growing under deciduous trees. L.d represents *Lactarius deliciosus*; L.h, *L. hepaticus*; L.z, *L. zonarius*; L.s, *L. subdulcis*; L.tor, *L. torminosus*; L.r, *L. rufus*; L.f, *L. fuliginosus*; L.v, *L. vellereus*; L.q, *L. quietus*; L.p, *L. piperatus*; L.t, *L. tabidus*; L.b, *L. blennius*; L.g, *L. glyciosmus*; L.tur, *L. turpis*; and L.py, *L. pyrogalus*. Black-coloured bars indicate species which displayed significant changes meanwhile white-coloured bars indicate species with non-significant changes in each of their fruiting aspects.

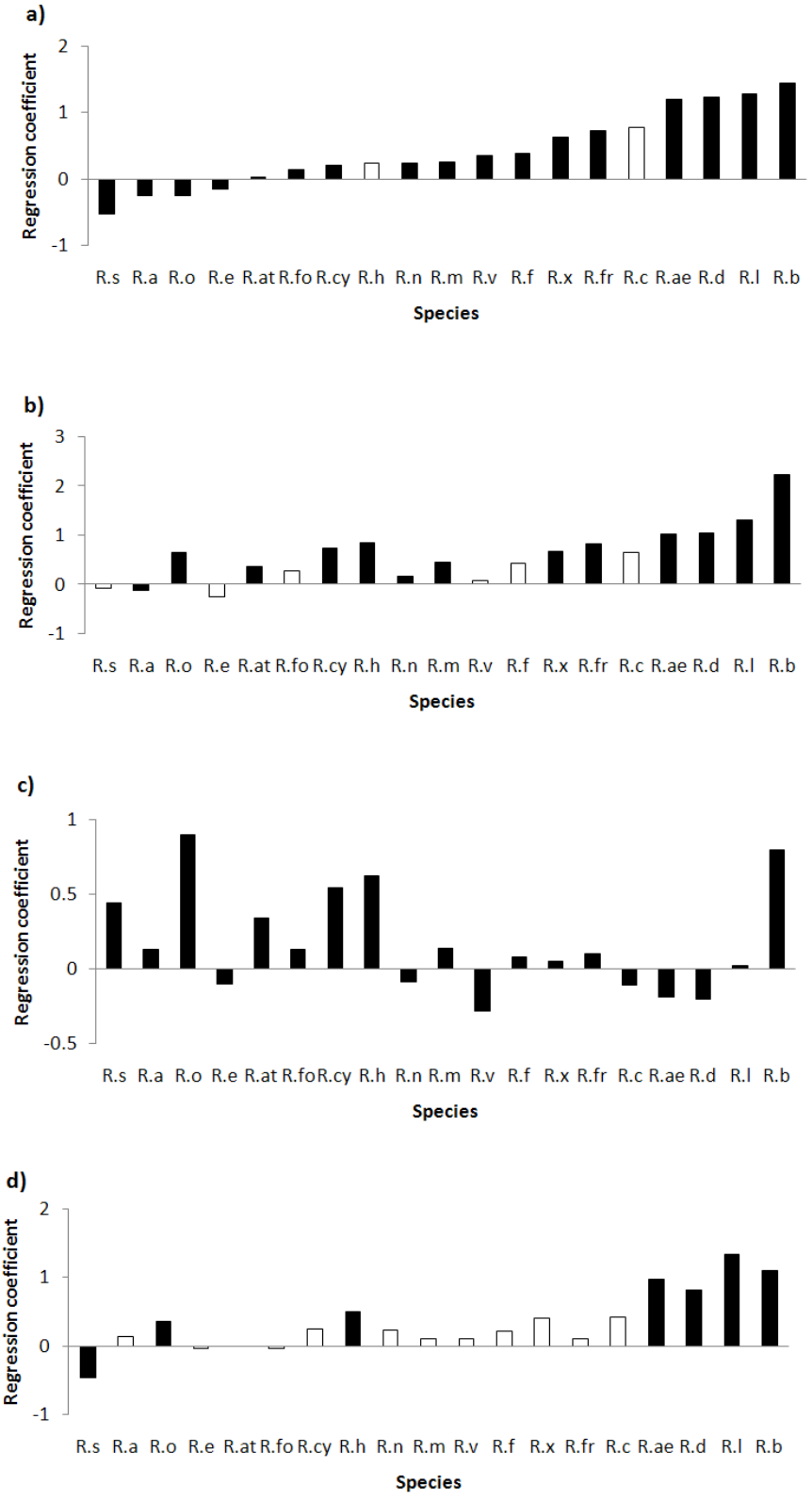


Figure 3.13 The change in a) first fruiting date, b) last fruiting date, c) length of fruiting date and d) average of fruiting date for 19 species of mycorrhizal *Russula* over 57 years growing under deciduous trees. R.s represents *Russula sardonia*; R.a, *R. adusta*; R.o, *R. ochroleuca*; R.e, *R. emetica*; R.at, *R. atropurpurea*; R. fo, *R. foetens*; R.cy, *R. cyanoxantha*; R.h, *R. heterophylla*; R.n, *R. nigricans*; R.m, *R. mairei*; R.v, *R. virescens;* R.f, *R. fellea;* R.x, *R. xerampelina*; R.fr, *R. fragilis*; R.c, *R. claroflava;* R.ae, *R. aeruginea*; R.d, *R. delica*; R.l, *R. lepida*; and R.b, *R. betularum*. Black-coloured bars indicate species which displayed significant changes meanwhile white-coloured bars indicate species with non-significant changes in each of their fruiting aspects.

b) Non mycorrhizal genera (Saprotrophic genera)

Genus *Clitocybe*

Similar to *Amanita*, most saprotrophic *Clitocybe* have shown earlier first appearance, with only three species showing delays, namely *C. dealbata*, *C. clavipes* and *C. phyllophila* (Figure 3.14a). Referring to the first two charts, five species namely *C. vibecina*, *C. rivulosa*, *C. gibba*, *C. nebularis* and *C. fragrans,* which have had early appearances, tend to have a delayed last fruiting date. Of these, only three species, *C. rivulosa*, *C. gibba* and *C. nebularis* have shown delays in their last fruiting date (Figure 3.14b). In response to the length of fruiting, most *Clitocybe* have shown significant changes in their fruiting season. 83% of the species have shown an extension with *C. vibecina* showing the greatest change with greater extension in its length of fruiting. Meanwhile, *C. phyllophila* has shown the greatest contraction in its fruiting season. Moreover, significant changes in the length of fruiting season were recorded in most *Clitocybe* except *C. brumalis* (Figure 3.14c). For average date of fruiting, *C. fragrans* showed the greatest change since the species had the most advanced average of fruiting compared to the other species in the genus (Figure 3.14d).

Genus *Collybia*

Five *Collybia* species were found to have an advanced first fruiting date while only one species showed a delayed first fruiting date. Significant changes in FFD were detected in all species except *C. confluens* (Figure 3.15a). Meanwhile, most species have shown delays in their LFD and only a species showed earlier LFD which was *C. fusipes*. It was noticeable that there were four species which have had earlier first fruiting showing a delayed in their last fruiting date. The earlier species were *C. dryophylla*, *C. peronata*, *C. butyracea* and *C. confluens* (Figure 3.15b). Therefore, this resulted in lengths of fruiting for four of these species showing a greater extension (Figure 3.15c). For average fruiting date, *C.*

confluens showed a significant change which explains the delays of the average appearance of this species (Figure 3.15d).

Genus *Mycena*

There was a wide range of response in first fruiting date in the twenty six recorded species in the genus. There are 15 species that show an advanced first fruiting with 11 of them showing significant changes in their FFD. In contrast, ten species were found to be delayed in their first appearance and eight of them have consistently changed their FFD. Meanwhile, there were three species that showed no change in their first fruiting date (Figure 3.16a). For last fruiting date, significant changes were detected in most species. There were four species which showed delayed first fruiting and a delayed last fruiting date too. These were *M. pelianthina*, *M. aetites*, *M. polyadelpha* and *M. rorida* (Figure 3.16b). The previous three species without any change in their first fruiting date that includes *M. pura*, *M. filopes* and *M. alcalina* were found to have changes in their last fruiting date. Here, *M. pura* and *M. filopes* were delayed while *M. alcalina* tended to be earlier in its last fruiting date (Figure 3.16b). Meanwhile, all *Mycena* have shown significant changes in their length of fruiting season except for *M*. *acicula*. There were 22 species that showed expansion of the fruiting season with *M.capillaris* having the greatest change (Figure 3.16c). For average of fruiting date, six out of 13 species which have earlier average of fruiting have shown significant changes. Similarly, half of the total species with delayed average of fruiting date also showed changes too. A similar response of first fruiting date was also detected in the average of fruiting for *Mycena.* Several earlier first fruiters tend to be earlier in their average of fruiting and the similar response was seen with delayed first fruiting date too (Figure 3.16d).

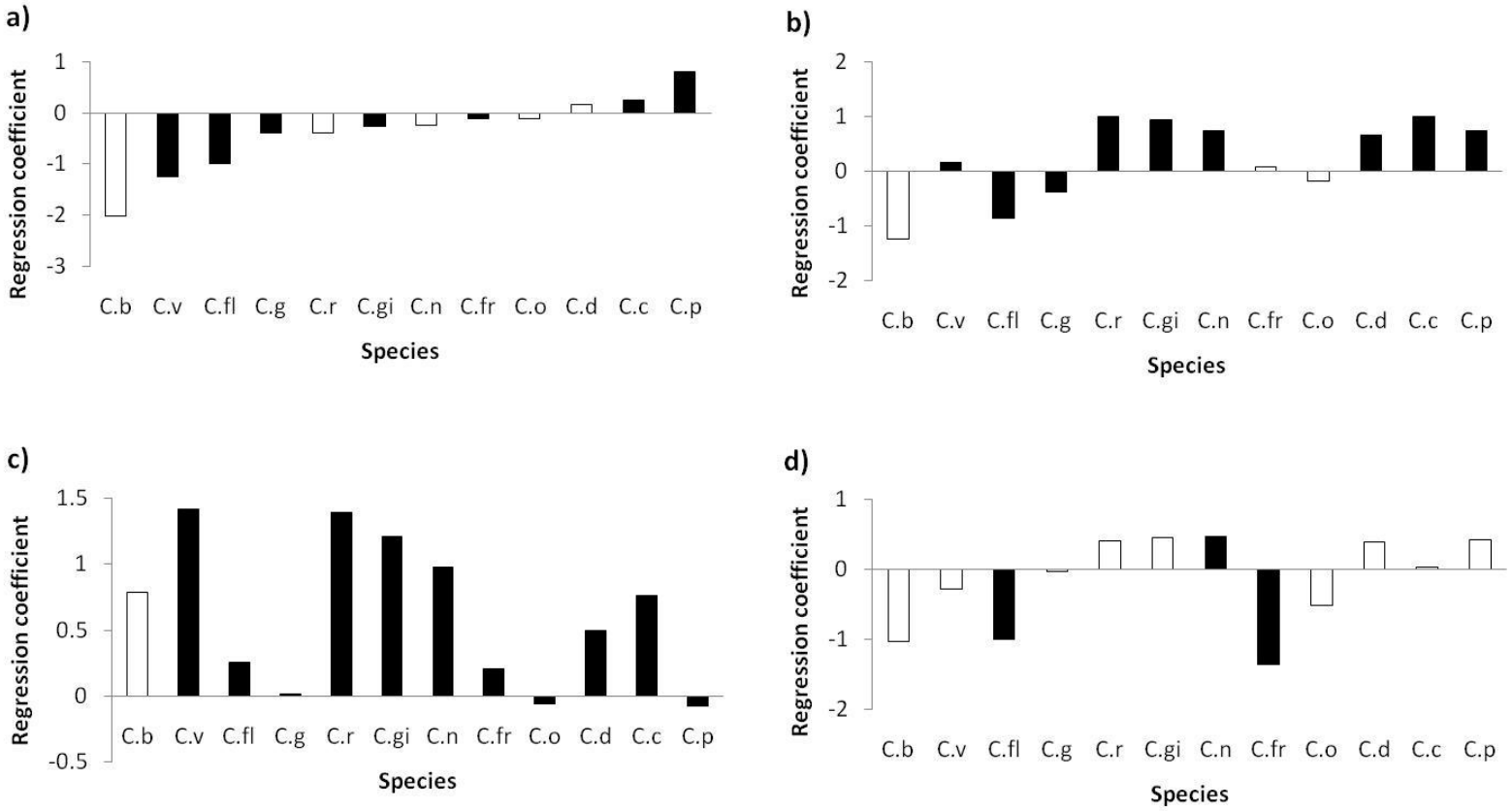


Figure 3.14 The change in a) first fruiting date, b) last fruiting date, c) length of fruiting date and d) average of fruiting date for 12 species of saprotrophic *Clitocybe* over the last 57 years. C.b represents *Clitocybe brumalis*; C. v, *C. vibecina*; C.fl, *C. flaccida;* C.g, *C. geotropa*; C.r, *C. rivulosa*; C.gi, *C. gibba*; C.n, *C. nebularis*; C.fr, *C. fragrans*; C.o, *C. odora*; C.d, *C. dealbata*; C.c, *C. clavipes*; and C.p, *C. phyllophila*. Black-coloured bars indicate species which displayed significant changes meanwhile white-coloured bars indicate species with non-significant changes on each of their fruiting aspects.

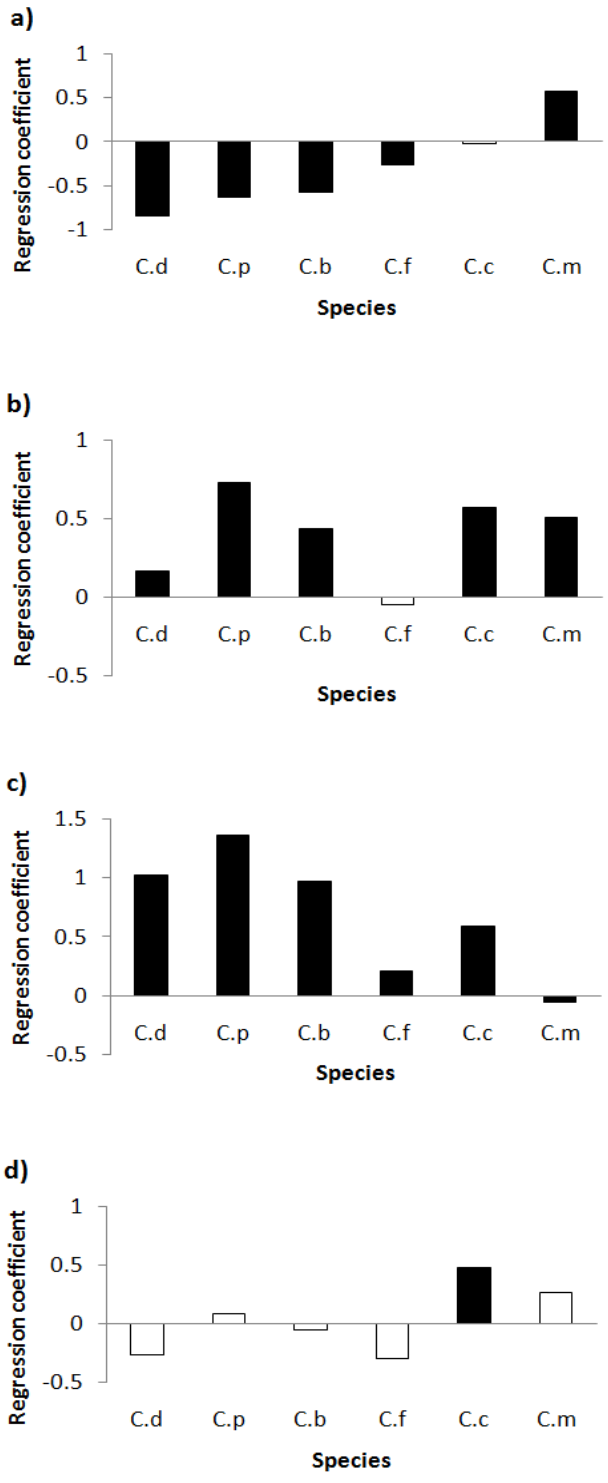


Figure 3.15 The change in a) first fruiting date, b) last fruiting date, c) length of fruiting date and d) average of fruiting date for 6 species of saprotrophic *Collybia* over the last 57 years. C.d represents *Collybia drophila*; C.p, *C. peronata*; C.b, *C. butyracea*; C.f, *C. fusipes*; C.c, *C. confluens;* and C.m, *C. maculata.* Black-coloured bars indicate species which displayed significant changes meanwhile white-coloured bars indicate species with non-significant changes on each of their fruiting aspects.

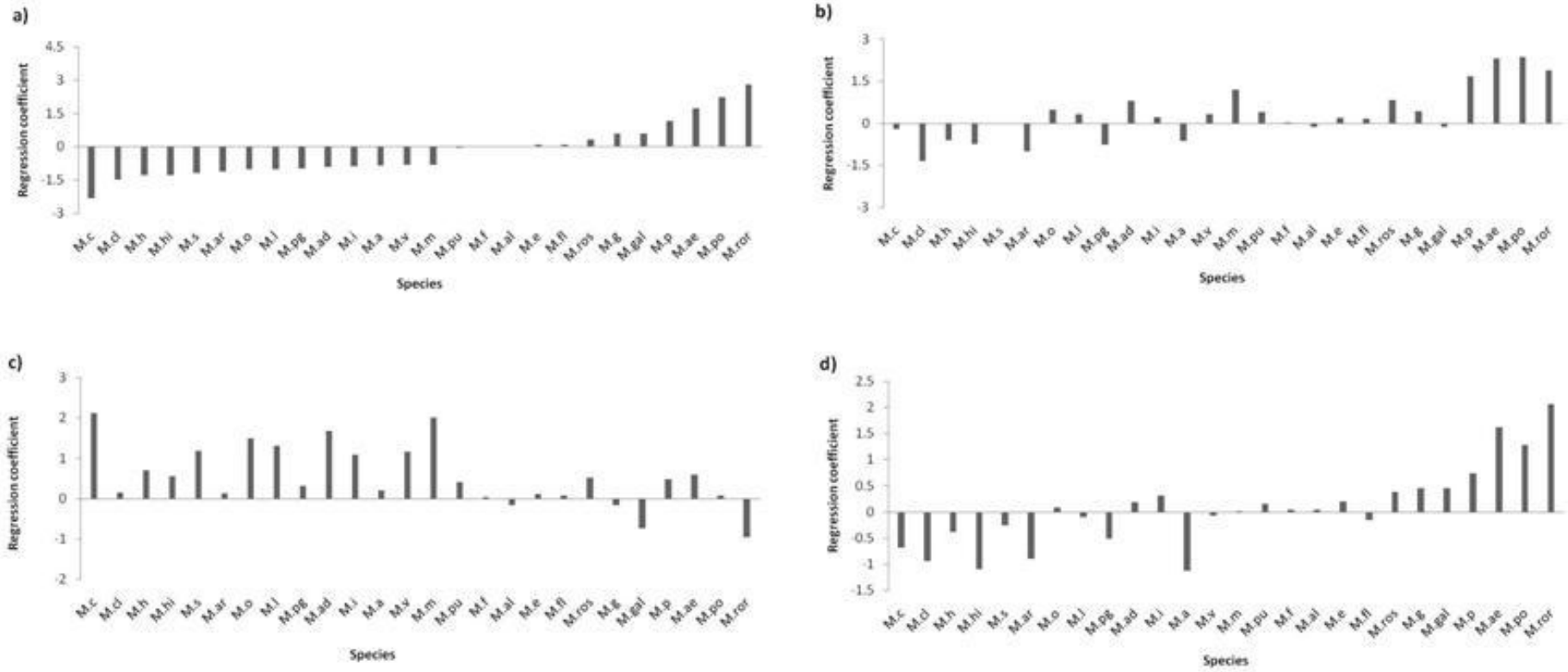


Figure 3.16 The change in a) first fruiting date, b) last fruiting date, c) length of fruiting date and d) average of fruiting date for 26 species of saprotrophic *Mycena* over the last 57 years. *M.c* represents *Mycena capillaries; M.cl, Mycena clavularis; M.h, Mycena haematopus; M.hi, Mycena hiemalis; M.s, Mycena speirea; M.ar, Mycena arcangeliana; M.o, Mycena olida; M.l, Mycena leptocephala; M.pg, Mycena polygramma; M.ad, Mycena adscendens; M.i, Mycena inclinata; M.a, Mycena acicula; M.v, Mycena vitilis; M.m, Mycena metata; M.pu, Mycena pura; M.f, Mycena filopes; M.al, Mycena alcalina; M.e, Mycena epipterygia; M.fl, Mycena flavoalba; M.ros, Mycena rosea; M.g, Mycena galericulata; M.gal, Mycena galopus; M.p, Mycena pelianthina; M.ae, Mycena aetites; M.po, Mycena polyadelpha;* and *M.ror, Mycena rorida.* Black-coloured bars indicate species which displayed significant changes meanwhile white-coloured bars indicate species with non-significant changes on each of their fruiting aspects.

3.4 Discussion

3.4.1 *Changes in fungal phenology*

Over 58 years, most ecological groups displayed changes in their fruiting aspects especially in their first fruiting date (FFD) and last fruiting date (LFD). Most groups have shown earlier appearance meanwhile, on the contrary, disappearance was more delayed at the end of the fruiting season for most of the groups in the study. The results of earlier FFD together with the delay of average last day that fruit bodies were seen have clearly resulted in the expansion of the overall fruiting season. The expansion of fungal fruiting in both directions in the UK is similar to the findings by Gange *et al*. (2007) but contrary to findings by Kauserud *et al*. (2008, 2012). These authors found that length of the overall fruiting season in Norway during the period 1940-2006 has been compressed. Perhaps, there could be site-specific factors, including precipitation, shading, soil conditions, nutrient concentrations and pathogens, that can act together with temperature to determine a species' phenology **(**Winder & Cloern 2010; Ibáñez *et al*. 2010). However, these hypotheses are yet to be tested and therefore further research should be undertaken to identify the real causes behind the differences.

The numbers of species in each ecological group showed great variation in all fruiting aspects from FFD, LFD, length of fruiting (RANGE) and the average of fruiting (MEAN). These variations are likely to be due to individualistic reactions of species towards environmental changes. Paleological studies suggest that the majority of species will respond individualistically to changes in climate (Huntley 1991; Hansen *et al*. 2001; Bush 2002; DeWan *et al.* 2010). Keith *et al*. (2009) have stated that significant evidence of species' responses to climate change was found in the fossil record from the Quaternary Period. These involve plants, insects and mammals. For fungi, individualistic responses could be caused by variations in each organism's requirement for environmental parameters such as temperature and rainfall (Voigt *et al*. 2003). This explanation is also supported by Treseder *et al*. (2003), Wolf *et al*. (2003) and Johnson

et al. (2005) who stated that the responses of fungi are specific to each species in terms of their responses to CO_2 enrichment which are beneficial for both plant and fungal symbiotic relationships (O'Neill 1994). Another example was research by Pinna *et al*. (2010) who found that elevated average soil temperature during a fruiting season delayed the initial fruiting date of *Catathelasma ventricosum* and *Leccinum peceinum* at Gaspé Peninsula in Québec, Canada. Moreover, these authors also discovered that extreme variation in soil temperature was found to reduce the length of fruiting for *Boletus edulis* and *Lactarius deterrimus.* Gange *et al*. (2007) and Kauserud *et al.* (2008, 2012) also agreed with the fact that these two parameters do affect fungal fruiting patterns, and in this respect, fungi can be seen as variable as other organisms. Even though weather conditions play a key role for most of the fruit body production, however, they do not completely explain the growth and productivity of wild mushrooms (Egli 2011). In fact, many factors interact with fungal fruiting in nature.

Variations in fruiting within the season could be a result of a highly controlled phenomenon determined by the plant (host) or the fungi themselves or their interaction, in response either to the flow of materials across the plant-fungus interface. For example, Högberg *et al*. (2001, 2010) showed that the biomass of fruiting bodies of mycorrhizal fungi is highly correlated with the rate of photosynthesis of host trees and the seasonal patterns of photosynthate allocation to roots. Therefore, patterns of fungal fruiting may correlate with photosynthetic activity and subsequent flux of photosynthates in forest trees. Meanwhile, biological cycles and the genetic background of species could also regulate the length of fruiting season (Guinberteau & Courtecuisse 1997; Baptista *et al.* 2010).

Climate change not only alters fungal phenology in the fruiting season. Climatic warming also tends to advance the onset of insect life cycles (Stange & Ayres 2010). Examples include the spruce beetle, *Dendroctonus rufipennis* which has shortening in the duration of its life cycle in some regions from 2 years to 1 year (Logan *et al.* 2003; Stange & Ayres 2010). Other examples include the advanced flight dates of Ephemeroptera (mayflies) in high altitude streams (Harper & Peckarsky 2006),

Odonata (dragonflies and damselflies) in the Netherlands (Dingemanse & Kalkman 2008) and Lepidoptera (butterflies and moths) in California (Forister & Shapiro 2003). Meanwhile, changes have also been reported in the phenology of birds with respect to the timing of migration and in average laying date (Crick 2004). Earlier trends for timing of spring arrivals were detected in many species (e.g. Forchhammer *et al*. 1998; Bradley *et al.* 1999; Loxton & Sparks 1999; Jenkins & Watson 2000; Sparks & Mason 2001; Gilyazov & Sparks 2002; Hüppop & Hüppop 2003). Meanwhile, last observations of birds have tended to become later, with a consequence that duration of stay on the breeding grounds has increased for some species (Sparks & Mason 2001; Gilyazof & Sparks 2002). Research has shown that laying date for birds is related to temperature and rainfall (Crick & Sparks 1999) while earlier shifting of an average lay date of a Tree Swallow species was due to the change in air temperature (Dunn & Winkler 1999). In other respects, Stevenson and Bryant (2000) suggested that the impacts of climate warming should be more obvious in smaller-sized species than in larger ones. This suggests that there may be physiological reasons for the response of an individual species to climate change (Crick 2004). Furthermore, phenological changes due to climate change also have been documented across other taxonomic groups, including timing of flowering and bud burst in plants, first appearance of butterflies, timing of phytoplankton blooms and choruses or spawning of amphibians (McCarty 2001; DeWan *et al.* 2010).

Further analysis on phenological aspects was continued by examining changes in FFD, LFD, RANGE and MEAN of each species over the 58 years of records. The analyses used in the study were similar to the methods applied by Gange *et al*. (2007). However there are differences between the study conducted by Gange *et al*. (2007) and the current study as they only conducted the analysis on 11 mycorrhizal species, recorded beneath both deciduous and coniferous tree hosts. Meanwhile, this study focuses on a comprehensive analysis that distinguishes ten ecological groups.

Of the ten groups analysed, only mycorrhizal species inhabiting deciduous trees, needle-leaf litter and wood-decay fungi showed changes in their FFD. These groups

with species that appear later in the season are showing trends to earlier fruiting while the reverse applied for early fruiters. Meanwhile, only mycorrhizal deciduous species showed changes in their LFD, with early growing species tending to have a delayed end of fruiting, and vice versa. This indicated that later fruiters in mycorrhizal deciduous species tend to fruit early in the season and have earlier last fruiting dates while the early fruiters started to fruit later in the season and tended to have later last fruiting dates. The physiological status of the plants could have an influence on this phenomenon. For mycorrhizal fungi, they depend on photosynthetically fixed carbon produced by their associated trees and also, the physiological state of host trees may well drive the growth of these fungi (Egli 2011). Further evidence for plants exerting control of fruiting in their mycorrhizal partners comes from an analysis of a 50 y old dataset which revealed that in the UK since 1958, fungi that are ectomycorrhizal with both conifers and deciduous leaves now fruit later in autumn co-incidental with the fact that deciduous trees now remain in leaf much longer than they used to (Gange *et al.* 2007; Baptista *et al*. 2010).

Species inhabiting needle litter in coniferous forests have shown responses in their length of fruiting season where the species that grow later in the season tend to have longer fruting seasons compared to species that appear in early season. Lehmann and Hudson (1977) compared fungal successions on needle groups fallen at different seasons in Britain. They studied the fungal successions on the needles fallen in early and late autumn and found little difference between them. According to Tokumasu (1998), climatic elements, especially air temperature, appeared to be one of the critical factors contributing to fungal seasonal changes in this type of forest. They suggested that sudden temperature drop may contribute to fungal succession. Tokumasu *et al.* (1996) indicated that in the beginning of autumn, most fungi that inhibit the surface layer of the litter can colonise freshly fallen needle. In addition, fungi with a relatively rapid mycelial growth rate under the temperature conditions of needle fall may often succeed in invasion of the freshly fallen needles.

3.4.2 Responses of genera that fruit at similar times

Another phenological aspect in fungal community structure examined was the investigation of responses of genera that fruit at similar times, on the assumption that species with similar taxonomic bases might respond in a similar manner. The most common genera in the study were the genera *Lactarius, Clitocybe, Inocybe, Amanita*, *Mycena* and *Russula* being the largest in terms of species number. The above genera were also commonly found in other studies e.g. Baptista *et al*. (2010).

Of the common genera recorded in the dataset, most were dominated by mycorrhizal species compared to the saprotrophs. There were differences between these two trophic groups. Saprotrophic fungi decomposing wood and litter (Rayner & Boddy, 1988) obtain energy by degrading dead organic matter (Lindahl *et al*. 2007). On the other hand, mycorrhizal fungi obtain their energy from symbioses relationship with their host plants and in return providing their plant hosts with soil-derived nutrients (Smith & Read 1997; Lindahl *et al.* 2007). To be exact, previous findings showed that saprotrophs require litter from (the) previous year(s) while mycorrhizal symbionts require photosynthate quickly exudated by young roots (Romell 1938, Last *et al*. 1979; Straatsma *et al*. 2001).

Similar results were also reported by Lagana *et al.* (2002) and Baptista *et al*. (2010) where the majority of their macrofungal species found were ectomycorrhizal species and the remaining were either saprotrophic and/or saprotrophic/parasitic. The high frequency of mycorrhizal species found in the records could be due to the age factor of the forests. Dighton & Mason (1985) has shown that the number of ectomycorrhizal species present in a given ecosystem is dependent on the host plant's age. Moreover, research by Luoma *et al*. (1991), Keizer & Arnolds (1994) and Smith *et al.* (2002) again reinforce the fact that the number of ectomycorrhizal species could increase gradually with host plant age.

Mycorrhizal species in the genera *Amanita, Inocybe, Lactarius* and *Russula* co-occur in woodlands and furthermore occupied similar ecological habits. – closely tied to their host phenology**.** Moreover, their fruit body production is often triggered by the movement of nutrients to the root, coincidental with leaf fall (Last *et al.* 1979). Although mycorrhizal species have similar ecological habits, not all species seem to respond in the same manner. Results have shown that very variable patterns were identified among the species, even within the same genus. Examples can be seen in the fruiting pattern shown by the genus *Amanita* and *Inocybe*. Even though these two species inhabit similar habitat – deciduous trees, both have shown a distinct patterns for all fruiting parameters recorded. The genus *Amanita* tends to fruit early in the season, while the genus *Inocybe* is likely to fruit later. Certainly, in terms of average of fruiting, *Inocybe* was found to fruit later date than *Amanita*. Perhaps, other features of forest habitats, such as composition, age and origin may influence the phenology of the species (Pinna *et al.* 2010). Last *et al.* (1981) discovered that one of the *Amanita* species, *A. muscaria* reacts more quickly to rainfall in mature forests than it does in young stands. Perhaps, the condition of the habitat in which the fungi grow involving different tree species and adaptation towards different environmental characteristics could be among the factors which may lead to the difference of responses between the genera within the same ecological group.

Overall, individualistic responses within genera were found in every case. Phenologically, there is much variability that may have results from differences in physiology, taxonomic position or the extent to which life history events are able to accelerate with warming (Thackeray *et al*. 2010). Furthermore, the experience of different warming trends due to variations in mean seasonal timing and microhabitat use could be another factor that could trigger the individualistic responses within genera. Alternatively, a different species or population in which phenological responses were driven/constrained by factors other than increases in temperature (Thackeray *et al.* 2010) could lead to the individual response of a species in terms of its fruiting.

In this study, mycorrhizal and saprotrophic groups of species have shown similar trends for each of their FFD, LFD, RANGE and MEAN. However, in years when warmer temperatures were present at the beginning of the fruiting season, most of the saprotrophic species reacted with earlier appearance, but most mycorrhizal species tend to have a later appearance. Another difference was seen in the average fruiting date wherein several saprotrophs began to fruit earlier in the later years of the study whereas most mycorrhizal species tend to have later average fruiting dates.

The influence of climate on the ecology of species may affect the physiology of organisms, as well as having indirect effects resulting from disruptions to food supply, changes in competitive interactions or influences on behaviour (McCarty 2001; Walther *et al*. 2002; Parmesan 2006). These effects alone or in combination could potentially impact the reproduction and/or survival, and therefore the long-term viability of fungal populations (DeWan *et al*. 2010). For instance, changes in competitive interactions between fungi could potentially influence the colonisation of substrates, its community composition and its organization (e.g. Brame & Flood 1983; Holmer & Stenlid 1996; Schmit 1999; Baar & Stanton 2000; Fryar *et al.* 2001). Moreover, Odum (1971) recognized that organic substances released into the environment during decomposition may have profound effects on the growth of other organisms within the same ecosystem. Therefore, any changes which happened along the process could affect the other organisms which rely on the supplies provided by the decomposer (fungi). Therefore, knowledge of fungal fruiting is important in understanding the functional roles of the fruit bodies in environment. Moreover, the results from this study are also relevant in a conservation context where further research on the dataset of rare species could be conducted. Findings from this study can also draw attention to anyone wanting to try to manipulate the yield of edible mushrooms in forests for industrial purposes. In addition, altered mushroom appearance suggests altered mycelial growth, which suggests altered competitive interactions between fungi. Could this lead to changes in community structure through host shift? This was the aim for my next study in *Chapter 4.*

Chapter 4

Do species expand and/or shift their hosts?

Note: parts of this chapter have been published as Gange *et al.* (2011)

4.1 Introduction

4.1.1 Associations between fungi and their hosts

The association between fungi and their hosts is important as it is one way to determine the occurrence and abundance of fungal species in the forest. Therefore, it is critical to study the relationship between fungi and their hosts (either plants or dead organic matter) and by observing each together, we may gain an understanding of fungal distributions in forest ecosystems. There are particular species of fungi that have an intimate relationship with living hosts (i.e. trees and other plants) and those that belong to this group are mycorrhizal, endophytic and pathogenic fungi. Mycorrhizas are a particular feature of forest ecosystems and associations between their host plants are characterised by a two-way beneficial interaction; the mycorrhizal fungi improve host performance by enhancing nutrient and water uptake from the soil and protecting host roots from pathogens (Smith & Read 1997; Ishida *et al*. 2007) while in exchange, the host provides fixed carbon to the fungi (Bruns *et al.* 2002). On the other hand, there is also a group of fungi that obtain their nutrients from non-living hosts (dead organic matter) in the ecosystem. This functional group is termed saprotrophic and species within this group consume dead organic matter that can be in different forms e.g. leaf litter, dead wood, dung and dead animals. Saprotrophic fungi are key regulators of nutrient recycling in forest ecosystems and thus play an important role in decomposition, carbon sequestration and nutrient recycling processes in all terrestrial ecosystems (Griffith & Roderick 2008).

4.1.2 Host specificity and host selectivity

Several previous studies of fruit body surveys have demonstrated various responses in fungal host specificity and host ranges from different mycorrhizal fungi. Bruns *et al*. (2002) found both fungal species and their associated plants (typically large woody species e.g. pines, oak, birches) that involved in ectomycorrhizal symbioses are derived from more than one common evolutionary ancestor with multiple origins of the symbiosis accounting for, at least, a large part of the pattern. Meanwhile, in wood-decay fungi, there is evidence of host selectivity of some species found in different environments, ranging from tropical wetlands, mangrove forests to deciduous and temperate forests (Boddy 2001; Boddy & Heilmann-Clausen 2008; Gilbert *et al.* 2008; Gange *et al*. 2011). Boddy (2001) stated that the causes of host selectivity of wood decay fungi are complex, including wood chemistry, wood microclimate, gaseous regime and the ways in which fungi become established. In addition, environmental factors limiting plant distribution may also contribute to selectivity (Gilbert *et al.* 2008).

Gange *et al.* (2011) suggested that the estimation of fungal host selectivity can be done by using the technique of species accumulation curves – as species diversity increases with sampling effort (Henderson 2008). This was supported by Unterseher *et al.* 2008 who have successfully applied a similar method, examining species occurence of wood decay fungi in their study. Earlier, Tofts & Orton (1998) who analysed 502 agarics and boleti species in Abernethy Forest, UK for 21 y demonstrated that total species accumulation curve still shows no convincing signs of reaching a limiting value (plateau) and concluded that the period of 21 y of recording was insufficient to reliably estimate the fungal biodiversity of the site. Despite these indications, this technique has never been applied to host range studies, let alone to make comparison between mycorrhizas and saprotrophic fungi.

4.1.3 Previous study

It is only in recent decades that mycologists have started to explore changes in fungal host associations, both in terms of extension of host range and also the shifting of hosts. Gange *et al.* (2011) discovered changes in the host range of a common species, *Auricularia auricularia-judae*. The species also has altered its phenology which has taken place since the late 1970s, with the first fruiting date (FFD) of *A. auricularia-judae* becoming significantly earlier. In the 1950s, the mean FFD was day 332 (28 November) while in the current decade, it has been day 257 (14 September). There was no change in its last fruiting date (LFD), however the earlier fruiting of the species has led to the expansion of its fruiting season (Gange *et al.* 2011). In addition, long term datasets of records of fungal fruit bodies are becoming available which are relevant for fungal host studies. The fact that fresh fruit bodies are ephemeral, the date of collection is likely to present good data for the purpose of this present study.

Specifically, this study aims (i) to explore host ranges in eight genera: *Amanita, Boletus, Clitocybe, Collybia, Inocybe, Lactarius, Mycena* and *Russula* and ii) to compare trendlines of host range of each species in every genus according to different groups based on their nutritional mode; the mycorrhizas and the saprotrophs. I hypothesized that these groups may show differences in their appearance, disappearance, length of fruiting and also in their average of fruiting. Findings of this study may highlight an important problem for those who want to predict biodiversity through extrapolation of a curve. Besides that, a thorough understanding of fungal-host associations also may be helpful in determining how changes in biological communities, brought by many potential aspects could affect the host ranges in macrofungal communities.

4.2 Methodology

The data set used for the study is that previously used in Chapter 3 of the thesis. Details about the data set are given in *Chapter 2* (Dataset Properties). In this chapter, common genera that were previously used in Chapter 4 were selected for the host

trend analysis. The aim was to identify species with altered host associations or species with expanded host ranges. For that reason, six genera namely *Amanita* (n=9), *Boletus* (n= 6),*Clitocybe* (n=7), *Collybia* (n=6), *Inocybe* (n= 4), *Lactarius* (n=11) and *Mycena* (n=18) species with their host records were examined for host trend analysis. Several number of species did not match those in the other chapter because the 'missing' species are only on one host and thefore excluded from the study. (N) indicates number of species represented by each of the genus. Additionally, two other genera, *Boletus* (n=7) and *Russula* (n=18) were also added to the analysis. For this study, all species in every genus were selected based on two aspects; i) commonly found within the same site in the data set and ii) has been recorded for more than 20 years of forays. For further analysis in host shift/expansion, species were also chosen if they had been found under at least two different tree species.

To analyse long-term trends in host ranges, the number of species found under different hosts were arranged into year order. Afterwards, the total number of hosts per year that each species was found under was calculated and the cumulative number of hosts was plotted as a species accumulation curve. To examine whether there were significant trends in host ranges for each species in every genus over time, the cumulative number of hosts was regressed against year as the independent variable using polynomial regression. Statistical analyses were performed using Unistat 6.0 with significance level of $P=0.05$.

Trends in host range for every species in each genus was later compared in two different functional groups namely saprotrophs and mycorrhizas. The genera included in the 'saprotrophs' were those that live off dead or decaying organic materials. Meanwhile, genera grouped under 'mycorrhizas' were those that form ectomycorrhizal associations.

4.3 Results

4.3.1 Host expansion

4.3.1.1 Mycorrhizal genera

Among the eight genera, five were classified as mycorrhizal namely *Amanita, Boletus, Inocybe, Lactarius* and *Russula.* In *Amanita*, the species that showed the highest cumulative number of hosts was *A. vaginata* where the species was found under ten hosts in the dataset (Figure 4.1i) followed by *A. rubescens* with seven hosts recorded (Figure 4.1a). The species with the least hosts recorded over time was *A. muscaria* (n=2) (Figure 4.1d). In general, all *Amanita* sp. showed a significant trend in their cumulative number of hosts over time (Table 4.1). In addition, more than 50% of the species in the group showed a significant asymptotic curve. This indicates that as time passed, species tend to be found under another host, until eventually no more new hosts were recorded as the curve reached a plateau. Therefore, after 58 y, sampling is likely to have detected most or all of the hosts with which these species are associated. The species that showed this pattern were *A. fulva* (Figure 4.1c), *A. pantherina* (Figure 4.1e), *A. phalloides* (Figure 4.1f), *A. rubescens* (Figure 4.1g) and *A. vaginata* (Figure 4.1i). On the contrary, two *Amanita* sp. showed increasing accumulation curve without asymptote e.g. *A. citrina* (Figure 4.1a) and *A. echinocephala* (Figure 4.1b). This indicates that the cumulated number of hosts that each species was found with over time has yet to achieve stability and still shows an increasing number. Meanwhile, for the other two species, *A. muscaria* and *A. strobiloformis* which also showed an accumulation curves without asymptote, these species only have two hosts and it is likely that this result is a statistical artefact.

In *Boletus*, the cumulative number of hosts for every species in the genus has changed significantly over time (Table 4.1). Similar to *Amanita*, two patterns of curves were found in the genus; the asymptotic curve and the non-asymptotic curve. The asymptotic curve was found only in *B. chrysenteron* (Figure 4.2b) and *B. edulis* (Figure

Table 4.1. Relationship between cumulative numbers of hosts where species were found upon over 58 y study.

	R^2 polynomial	Fvalue	Fprobability	d.f
Amanita				
A. echinocephala	0.7689	63.21	<0.001	2,38
A. phalloides	0.8111	90.18	<0.001	2,42
A. strobiloformis	0.5503	23.252	<0.001	2,38
A. vaginata	0.8464	115.682	<0.001	2,42
A. citrina	0.6649	41.662	<0.001	2,42
A. fulva	0.9032	256.69	<0.001	2,55
A. muscaria	0.7962	105.49	<0.001	2,54
A. pantherina	0.7654	66.885	<0.001	2,41
A. rubescens	0.8455	150.464	<0.001	2,55
Boletus				
B. badius	0.7319	57.325	<0.001	2,42
B. chrysenteron	0.8783	198.395	<0.001	2,55
B. edulis	0.8674	134.135	<0.001	2,41
B. luridiformis	0.8956	171.562	<0.001	2,40
B. luridus	0.9362	366.846	<0.001	2,50
B. subtomentosus	0.9362	403.154	<0.001	2,55
Clitocybe				
C. fragrans	0.9566	462.599	<0.001	2,42
C. geotropa	0.9521	407.28	<0.001	2,41
C. gibba	0.8606	132.698	<0.001	2,43
C. nebularis	0.9684	841.411	<0.001	2,55
C. phyllophila	0.9514	420.441	<0.001	2,43
C. rivulosa	0.793	99.595	<0.001	2,52
C. vibecina	0.9642	740.581	<0.001	2,55
Collybia				
C. butyracea	0.9526	532.973	<0.001	2,53
C. confluens	0.8723	146.851	<0.001	2,43
C. dryophila	0.9504	478.981	<0.001	2,50
C. fusipes	0.7288	73.893	<0.001	2,55
C. maculata	0.915	231.401	<0.001	2,43
C. peronata	0.9659	779.912	<0.001	2,55
Inocybe				
I. asterospora	0.9294	263.154	<0.001	2,40
I. flocculosa	0.7591	63.013	<0.001	2,40
I. geophylla	0.9403	417.597	<0.001	2,53
I. rimosa	0.962	670.553	<0.001	2,53
Lactarius				
L. deliciosus	0.6455	32.782	<0.001	2,36

L. hepaticus	0.8862	163.609	<0.001	2,42
L. quietus	0.8216	94.436	<0.001	2,41
L. rufus	0.8166	122.481	<0.001	2,55
L. subdulcis	0.7956	81.756	<0.001	2,42
L. tabidus	0.9151	226.243	<0.001	2,42
L. torminosus	0.8819	201.536	<0.001	2,54
L. turpis	0.421	15.27	<0.001	2,42
L. vellereus	0.8846	210.716	<0.001	2,55
L. zonarius	0.4513	20.566	<0.001	2,50
Mycena				
M. adscendens	0.9427	320.721	<0.001	2,39
M. alcalina	0.2771	6.901	0.003	2,36
M. capillaris	0.6262	19.265	<0.001	2,23
M. epipterygia	0.6391	37.193	<0.001	2,42
M. filopes	0.95	512.504	<0.001	2,54
M. galericulata	0.9426	451.822	<0.001	2,55
M. galopus	0.9382	318.977	<0.001	2,42
M. pura	0.8922	215.227	<0.001	2,52
M. galopus var. nigra	0.9578	442.348	<0.001	2,39
M. haematopus	0.8863	144.21	<0.001	2,37
M. hiemalis	0.953	415.955	<0.001	2,41
M. inclinata	0.945	464.067	<0.001	2,54
M. leptocephala	0.8791	152.703	<0.001	2,42
M. luteoalba	0.9518	404.553	<0.001	2,41
M. metata	0.958	615.291	<0.001	2,54
M. olida	0.9297	118.985	<0.001	2,18
M. pelianthina	0.8164	84.477	<0.001	2,38
M. polygramma	0.8923	174.027	<0.001	2,42
Russula				
R. adusta	0.5336	23.449	<0.001	2,41
R. aeruginea	0.5435	24.405	<0.001	2,41
R. atropurpurea	0.9047	261.003	<0.001	2,55
R. claroflava	0.773	69.815	<0.001	2,41
R. cyanoxantha	0.8954	235.425	<0.001	2,55
R. delica	0.8439	137.857	<0.001	2,51
R. emetica	0.8539	152.014	<0.001	2,52
R. fellea	0.8576	117.415	<0.001	2,39
R. foetens	0.8418	111.767	<0.001	2,42
R. fragilis	0.9208	284.79	<0.001	2,49
R. heterophylla	0.8955	179.904	<0.001	2,42
R. nigricans	0.8737	138.344	<0.001	2,40
R. ochroleuca	0.973	990.283	<0.001	2,55
R. sardonia	0.8554	156.729	<0.001	2,53
R. virescens	0.4282	15.355	<0.001	2,41
R. xerampelina	0.8424	109.579	<0.001	2,41

and *B. subtomentosus* (Figure 4.2f) have shown the highest number of hosts (n=12) in the 58 y. Both species were commonly found under *Picea abies (Norway spruce*), *Fagus sylvatica (Common Beech), Quercus robur (*English Oak*), Pinus sylvestris* (Scots Pine) 4.2.c) while the remaining species showed the non-asymptotic curve. *B. chrysenteron* (Figure 4.2b) and eight rarer hosts. The final host added for *B. chrysenteron* was *Betula pendula* (Silver Birch) meanwhile *B. subtomentosus* was found under *Prunus* sp. (Cherry), which was recorded in 2003.

Unlike *Amanita* and *Boletus*, the genus *Inocybe* only showed one pattern for all four species present in the group, which was the non-asymptotic curve. The trend line did not show any signs of approaching an asymptote and therefore, their cumulative numbers of hosts still have the potential to increase after year 2008. Significant trends were found in all four *Inocybe* sp. (Table 4.1) and among these species, *I. geophylla* and *I. rimosa* displayed the highest cumulative number of hosts, being found under 16 different hosts (Figure 4.3c,d). Both species were mostly found under *F. sylvatica, Q. robur, Acer campestre* (Maple), *B. pendula* (Silver Birch) and *Corylus avellana* (Hazel).

Similar to the previous genera, all species in the genus *Lactarius* showed significant changes in their cumulative number of hosts (Table 4.1). 80% of the total species showed an asymptotic curve, indicating that as sampling effort increased, so did the cumulative number of hosts, until they achieved a plateau in which no more hosts were recorded. The species with the highest cumulative number of hosts was *L. tabidus,* which was found under six trees including *Q. robur , B. pendula*, *Castanea* sp. (Chestnut), *C. avellana*, *F. sylvatica* and *Fraxinus excelsion*. (Ash) (Figure 4.4f).

Meanwhile, the cumulative number of hosts for each *Russula* sp. has also changed significantly over time (Table 4.1). 56% of the total species in the genus showed continuous expansion in their host ranges including *R. adusta* (Figure 4.5a)*, R. atropurpurea* (Figure 4.5c)*,* and *R. cyanoxantha* (Figure 4.5e). Only seven *Russula* sp.

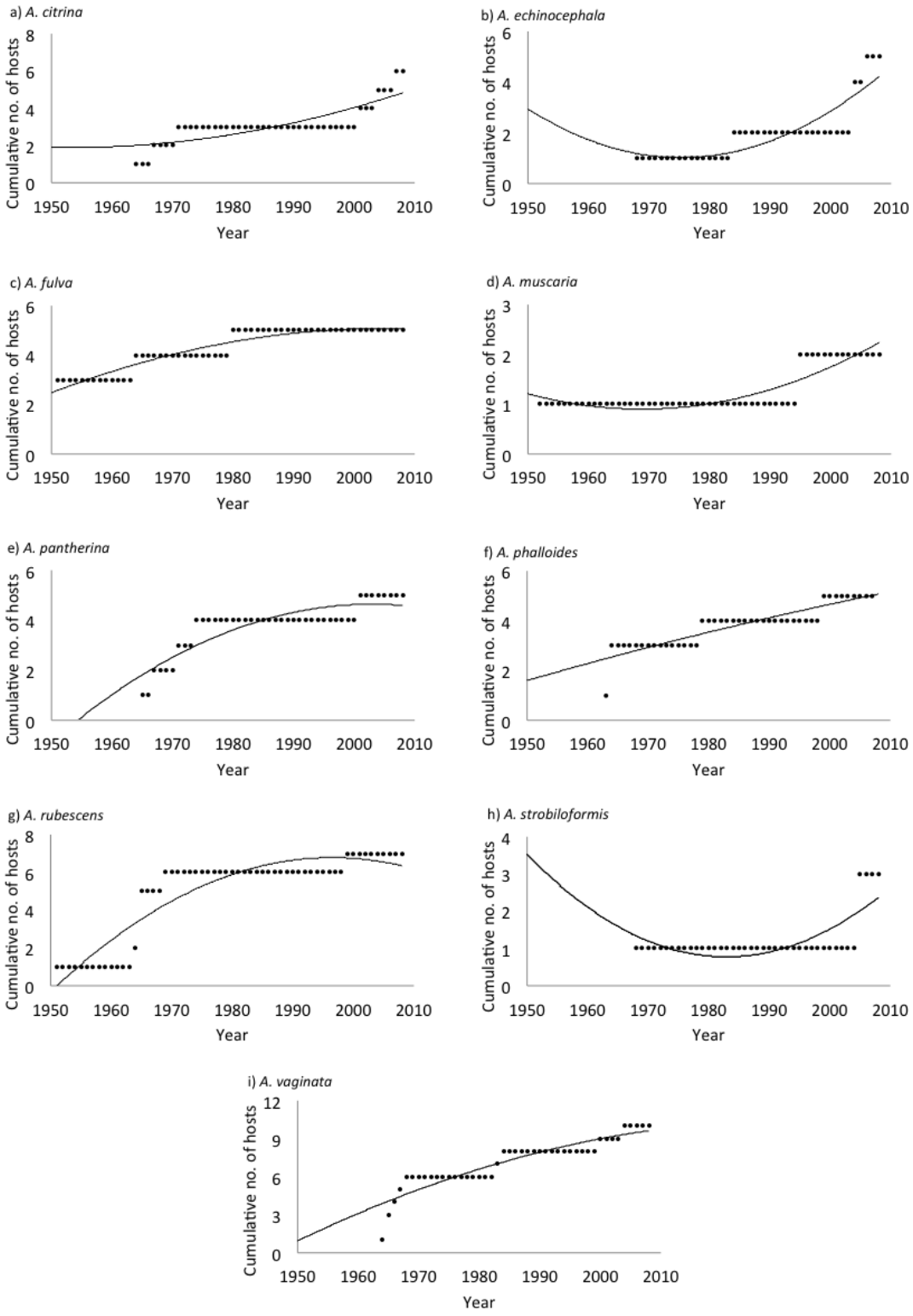


Figure 4.1(a-i) The cumulative number of hosts for *Amanita* sp. over the 58 y study. The trend lines indicate significant changes in the cumulative number of hosts over time.

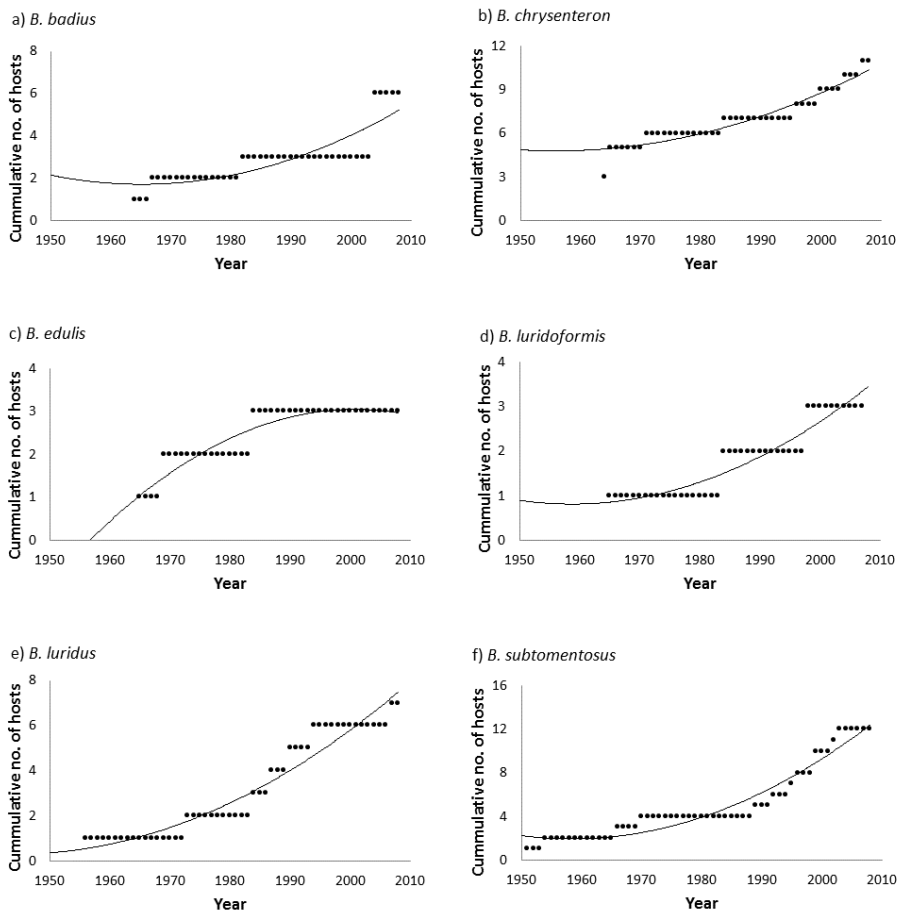


Figure 4.2(a-g). The cumulative number of hosts for *Boletus* sp. over the 58 y study. The trend lines indicate significant changes in the cumulative number of hosts over time.

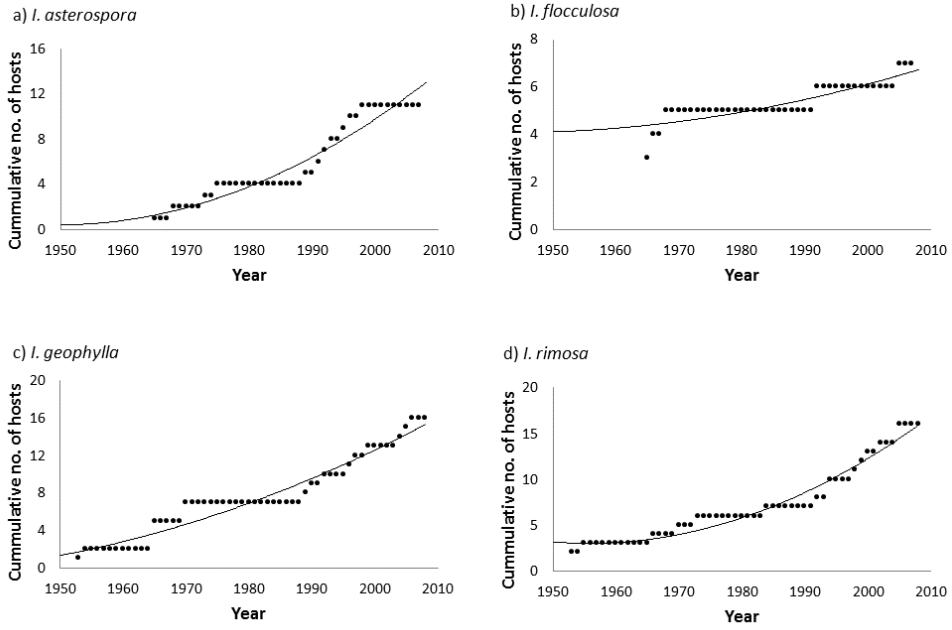


Figure 4.3(a-d) The cumulative number of hosts for *Inocybe* sp. over the 58 y study. The trend lines indicate significant changes in the cumulative number of hosts over time.

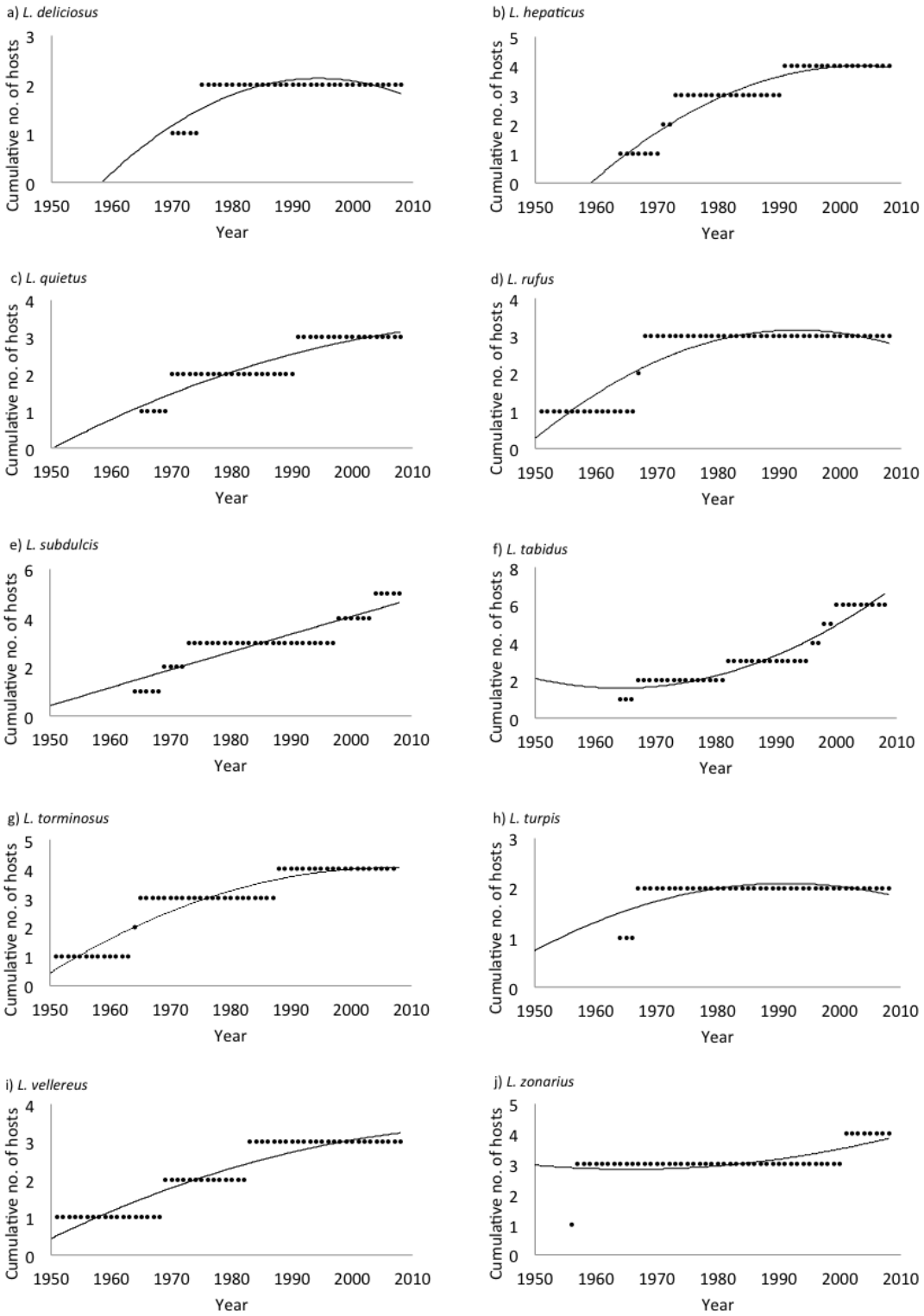


Figure 4.4(a-j) The cumulative number of hosts for *Lactarius* sp. over the 58 y study. The trend lines indicate significant changes in the cumulative number of hosts over time.

showed a plateau curve including *R. claroflava* (Figure 4.5d) and *R. virescens* (Figure 4.5o). However, these two species were only seen in two hosts in 57 years compared to the other *Russula* sp. Therefore, *R. claroflava* and *R. virescens* were likely to be sampling artefacts rather than biological changes.

4.3.1.2 Saprotrophic genera

There were three genera of saprotrophs analysed namely *Clitocybe, Collybia* and *Mycena*. Among seven species in the genus *Clitocybe*, six (86%) species showed the non-asymptotic curve (Figure 4.6). Meanwhile, one species (*C. vibecina*) showed an opposite trend line indicating that the species accumulations curve appeared to achieve a plateau (Figure 4.6g). Above all, every *Clitocybe* sp., has shown a significant trend in the cumulative number of hosts across 57 yr (Table 1). Furthermore, most of the species were commonly found under *F. sylavtica, Q. robur, P. sitchensis* and *Corylus* sp. Unlike other *Clitocybe* sp. that showed an increase in hosts over time, *C. rivulosa* displayed the least number of hosts where it was recorded to be seen only on grass and pathways (Figure 4.6f).

A similar trend was also seen in the genus *Collybia* where the majority of species displayed non-asymptotic curves. These were *C. butyracea* (Figure 4.7a)*, C. confluens* (Figure 4.7b)*, C. dryophila* (Figure 4.7c)*, C. fusipes* (Figure 4.7d) and *C. peronata* (Figure 4.7f). Only one species showed a different accumulation curve, (*C. maculata*) with an asymptote in its cumulative number of hosts across 42 years of records (Figure 4.7e). The trend line for *C. maculata* showed that in early records of the cumulative number of hosts for the species, new hosts were mostly recorded one after another in a short period of time. For example, the first host tree that *C. maculata* was found beneath was *B. pendula* which was recorded in 1963, however, a year after, the species was seen in another host, *P. sitchensis* followed by *Calluna vulgaris* (Heather) in the year 1966 and under *Pteridium aquilinum* (Fern) a year after. All *Mycena* sp. showed accumulation curves without an asymptote e.g. *M. adscendens* (Figure 4.8a)*, M. filopes* (Figure 4.8e)*, M. galericulata* (Figure 4.8f) and *M. galopus* (Figure 4.8g).

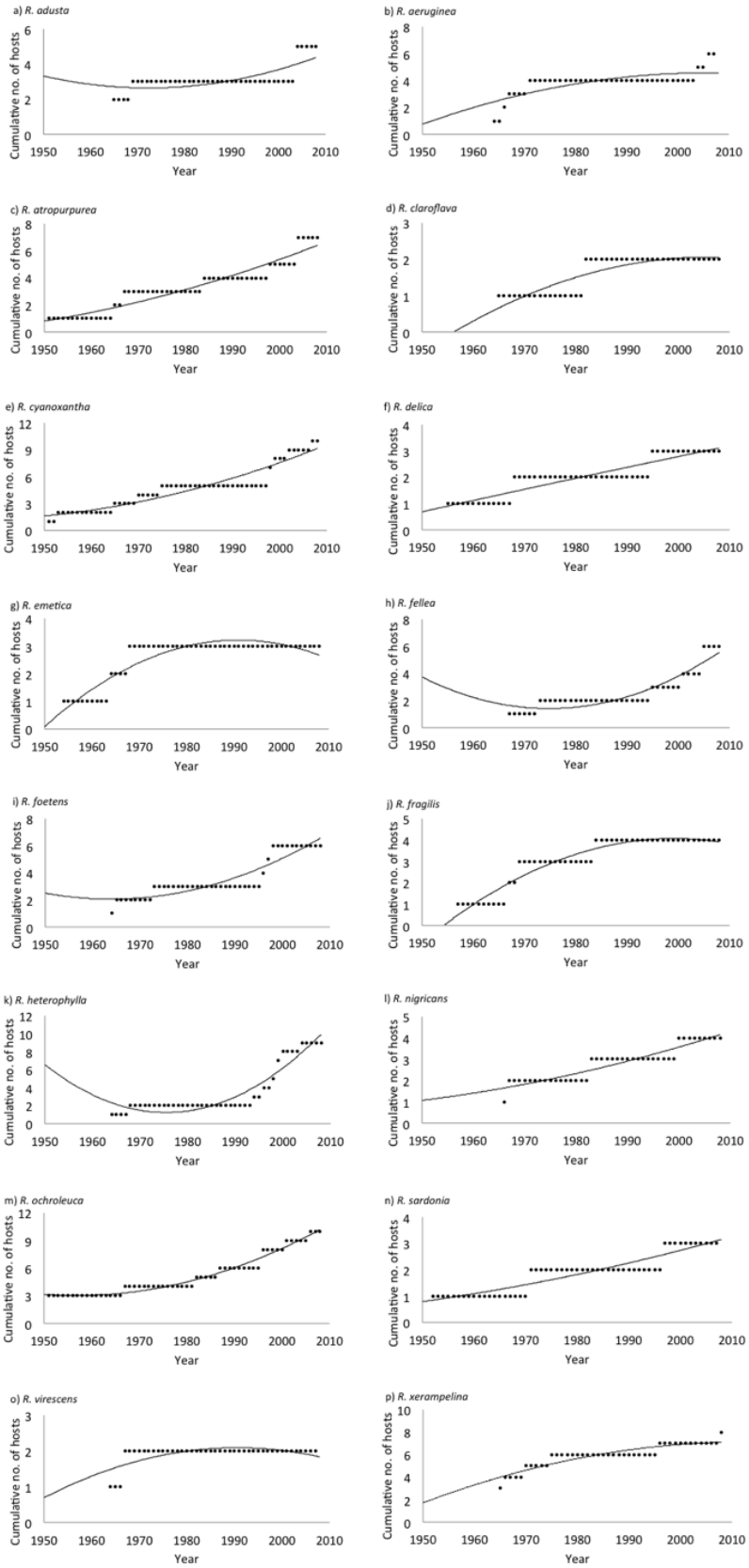


Figure 4.5(a-p) The cumulative number of hosts for *Russula* sp. over the 58 y study. The trend lines indicate significant changes in the cumulative number of hosts over time.

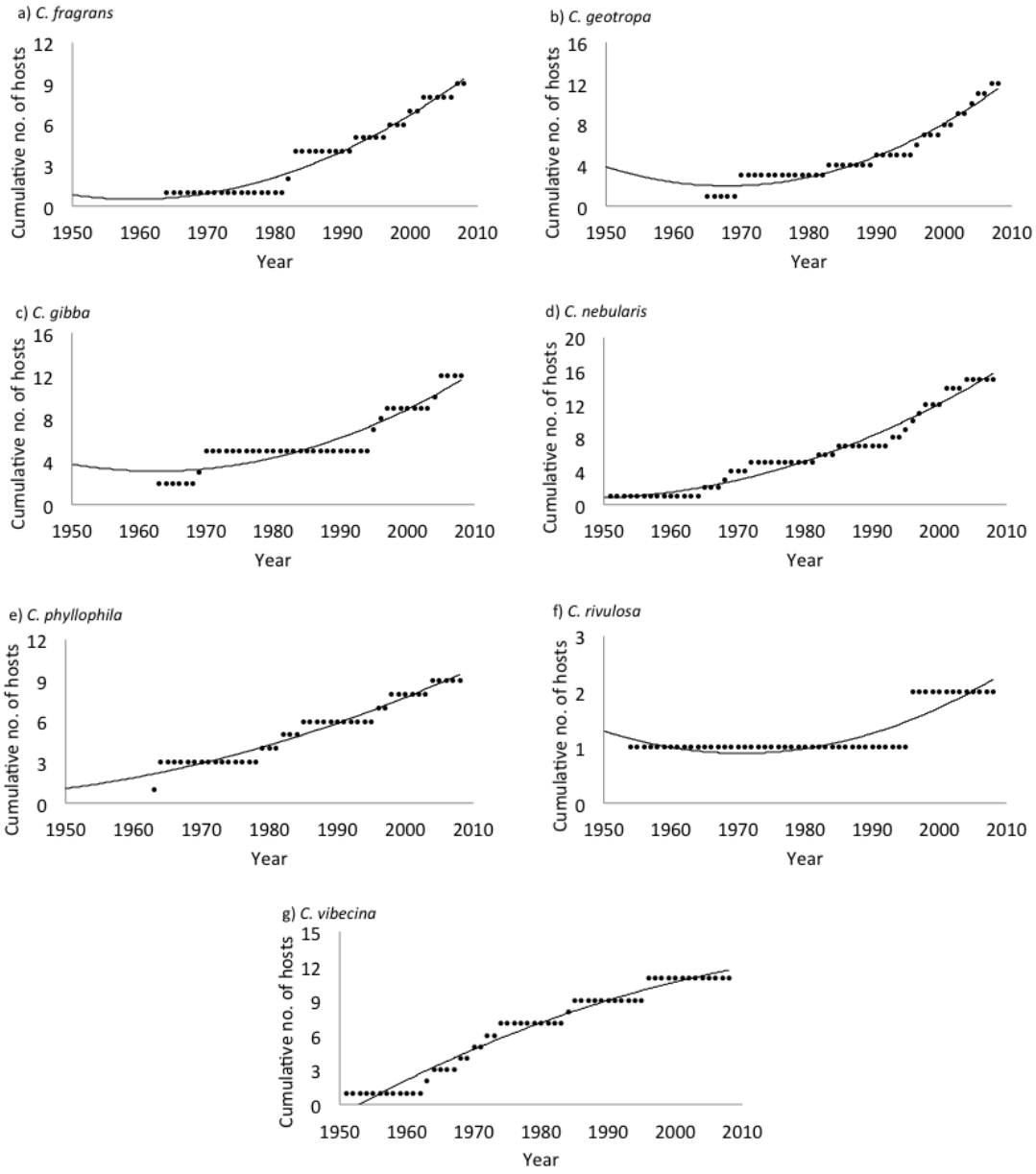


Figure 4.6(a-g) The cumulative number of hosts for *Clitocybe* sp. over the 58 y study. The trend lines indicate significant changes in the cumulative number of hosts over time.

commonly found under two host trees (*F. sylvatica* and *Q. robur*) but as time passed were found in many more hosts.

The genus *Mycena* had the highest number of species analysed in comparison to the other genera. All the species in the genus showed a significant trend in their cumulative number of hosts and all of them appeared under more than two host trees throughout the recording time (Figure 4.8, Table 1). 78% of the total species tended to

M. metata was the species with the most cumulative number of hosts recorded (n= 18) since 1951. This species was firstly seen in grass before later being found under *F. sylvatica, Q. robur, B. pendula*, *Cedrus* sp. etc. In contrast, four *Mycena* species were found to display asymptotic curves, and these were *M. alcalina* (Figure4.8b)*, M. capillaris* (Figure 4.8c)*, M. epipterygia* (Figure 4.8d) and *M. olida* (Figure 4.8p). Among these species, *M. olida* showed a narrower accumulation curve compared to the other *Mycena* sp. as the species was only discovered in 1988, three decades after the recordings started.

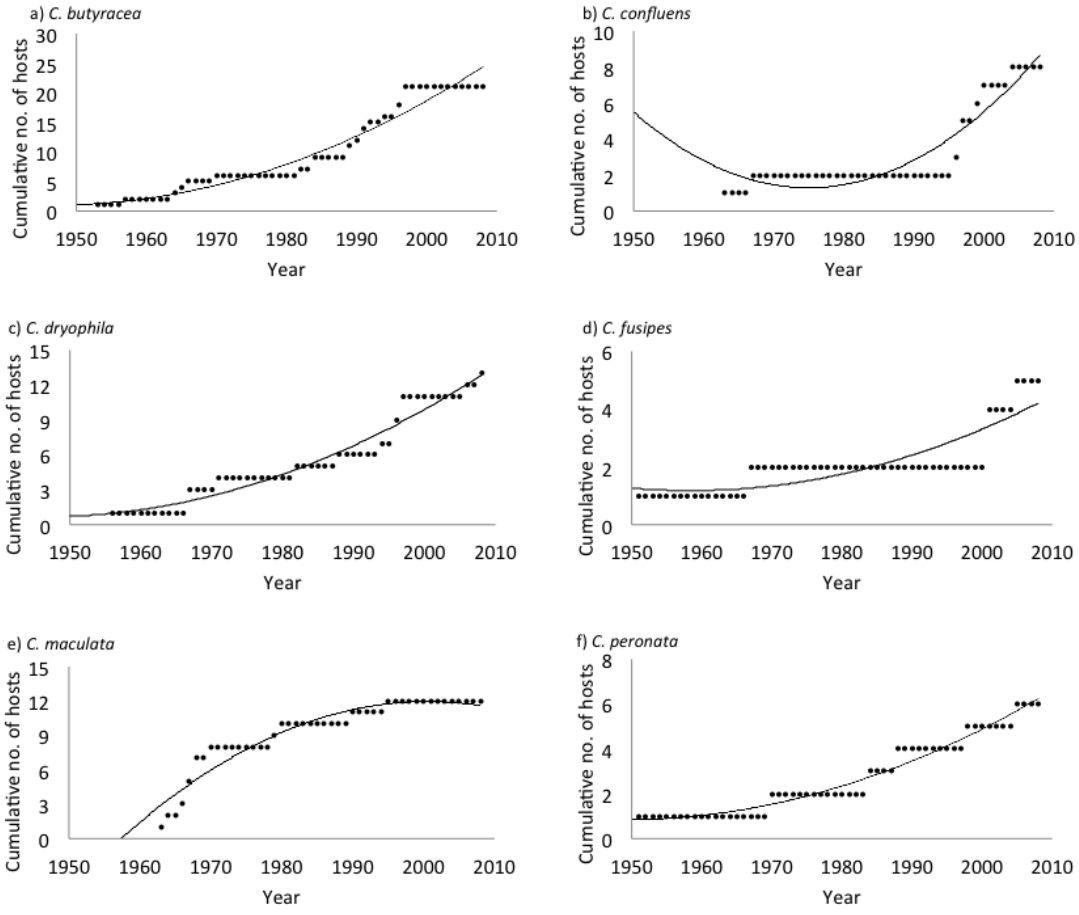


Figure 4.7(a-f) The cumulative number of hosts for *Collybia* sp. over the 58 y study. The trend lines indicate significant changes in the cumulative number of hosts over time.

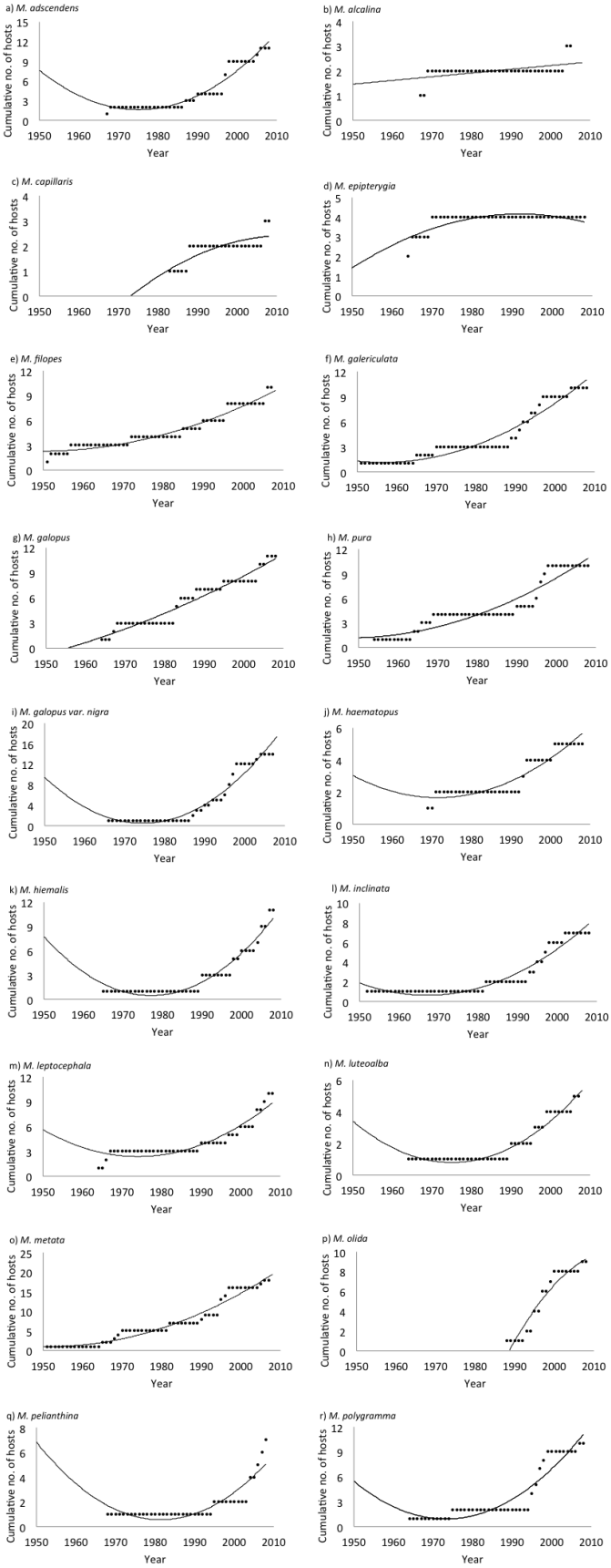


Figure 4.8(a-r) The cumulative number of hosts for *Mycena* sp. over the 58 y study. The trend lines indicate significant changes in the cumulative number of hosts over time.

In general, most species belonging to saprotrophic genera tend to show accumulation curves without asymptotes compared to the asymptotic accumulation curve (Table 4.2) suggesting that the rate of cumulative number of fungal host is still proceeding in a more-or-less linear fashion, without showing any signs of leveling off.

Table 4.2 Summary of the number of species that grouped into two different functional groups, mycorrhiza and saprotrophs based on their pattern of accumulation curves. It can be seen that while only 19% of saprotrophic species showed an asymptotic curve, in mycorrhizas, this proportion was 48%. The difference in proportions between the two groups was significant (χ^2 = 6.5, d.f. =1, $p < 0.05$).

	Asymptotic. curve	**Non-asymptotic curve**
Mycorrhiza	22	24
Saprotrophs	6	25

4.3.2 Host expansion and/or shift

4.3.2.1 Mycorrhizal genera

Among the genus *Amanita*, four of the species namely *A. fulva* (Figure 4.9c)*, A. pantherina* (Figure 4.9e)*, A. rubescens* (Figure 4.9g) and *A. vaginata* (Figure 4.9i) have shown significant trends in the proportion of records found under their dominant host. *A. fulva* has been found under a total of five hosts (Figure 4.1c), and it has been most commonly found under *B. pendula.* However, over time, it has become more common under this host (Figure 4.9c) while becoming less common under *Q. robur* (Figure 4.10a). A*. fulva* has been found more commonly under *B. pendula* since it was first recorded in the 1950s (Figure 4.9c). Meanwhile, the second common host which *A. fulva* was found to fruit beneath was *Q. robur* (Figure 4.10b). This host has shown a contrasting trendline to *B. pendula*, suggesting that *A. fulva* has been getting rarer under *Q. robur.* Both host records for *B. pendula* and *Q. robur* were best fitted to a second order polynomial with time compared to a linear function (*B. pendula*: $F_{2,40}$=

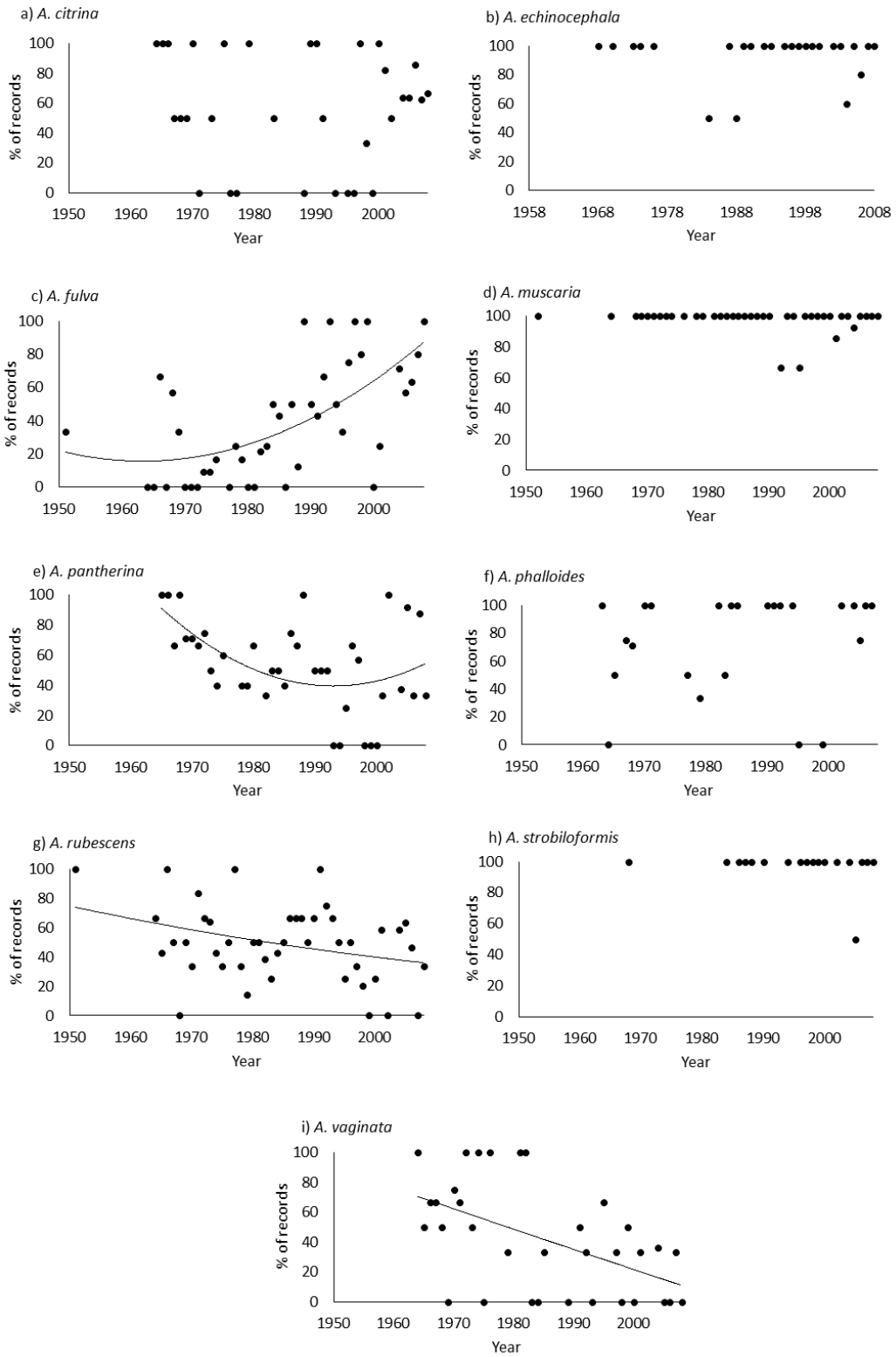


Figure 4.9(a-i) The proportion of fruiting records for each *Amanita* sp. found under their dominant host. a) *A. citrina* (Host: *Q. robur*), b) *A. echinocephala* (Host: *F. sylvatica*), c) *A. fulva* (Host: *B. pendula*), d) *A. muscaria* (Host: *B. pendula*), e) *A. pantherina* (Host: *Q. robur*), f) *A. phalloides* (Host: *Q. robur*), g) *A. rubescens* (Host: *Q. robur*), h) *A. strobiliformis* (Host: *F. sylvatica*) and i) *A. vaginata* (Host: *Q. robur*). The trend lines indicate significant changes in the proportions of records over time.

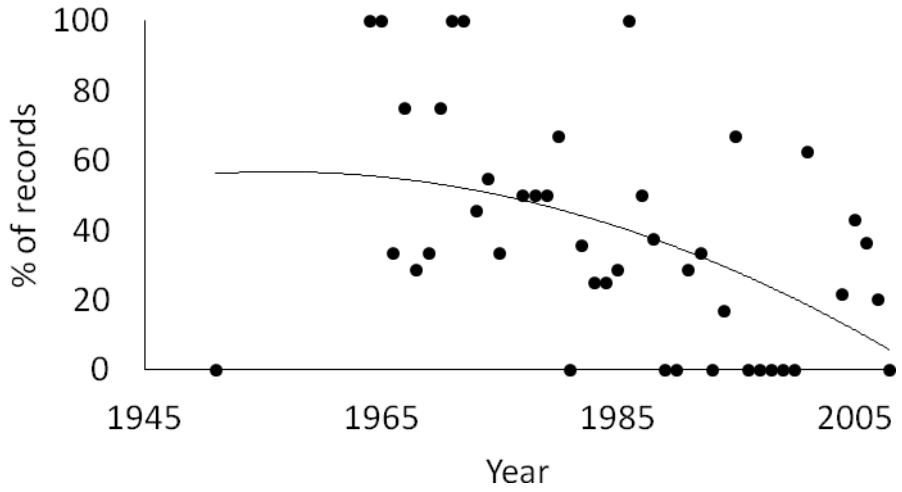


Figure 4.10 The proportion of fruiting records for *A. fulva* found in each year under *Q. robur.*

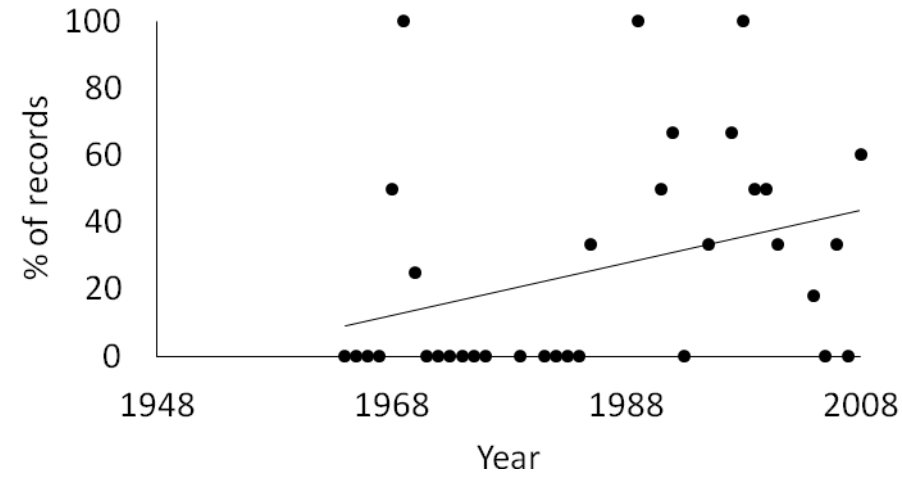


Figure 4.11 The proportion of fruiting records for *A. vaginata* found in each year under *F. sylvatica*.

11.32, $P < 0.01$, $R^2 = 36\%$; *Q. robur*: $F_{2,40} = 5.43$, $P < 0.01$,$R^2 = 21\%$). Another *Amanita* sp. that showed a significant interaction between the dominant host and its second most common host was *A. vaginata.* This species has been getting rarer under *Q. robur* (Figure 4.9i) but has become commoner under *F. sylvatica* (*Q. robur*: $F_{1,32}= 10.3$, $P \leq 0.05$, $R^2= 24\%$; *F. sylvatica*: $F_{1,32}= 4.48$, $P \leq 0.05$, $R^2= 12\%$) (Figure 4.11). *A. pantherina* (most commonly found under *Q. robur*) has shown a decline in its proportion of fruiting records under this tree over 40 years (Figure 4.9e). A similar pattern was also observed for *A. rubescens* (Figure 4.9g). Although these two species showed significant changes in the proportion of fruiting records under their dominant host, *Q. robur*, however, no significant changes were found with the other hosts where these species were recorded.

In *Boletus*, only three species, namely *B. chrysenteron* (Figure 4.12b), *B. luridiformis* (Figure 4.12d) and *B. luridus* (Figure 4.12e) displayed significant changes in the proportion of records for each species found under their dominant host. Over 58 y, *B. chrysenteron* has been found under 12 hosts (Figure 4.12b) and the species was most commonly found under *Q. robur* (Figure 4.12b). There has been an increase in the proportion of records of *B. chrysenteron* found fruiting under *Q. robur*, which suggests that the species was getting commoner under this host over time. A similar pattern was also seen in *B. luridiformis* and *B. luridus*. These two species have become commoner under *F. sylvatica* since the 1960s compared to the other hosts. However, there were no signs of these shifting hosts as there were no significant relations found in other common hosts where each species was found.

There was a significant decrease in the proportion of records of *I. asterospora* found under *Q. robur* (Figure 4.13a) through time. Although *Q. robur* appeared to be the dominant host for *I. asterospora* in its early records in 1960s, the species has become rarer beneath this tree as the years have passed. However, within the same period, the species has become commoner under another host tree, *F, sylvatica* (*Q. robur*: $F_{2,29}= 7.32$, $P \leq 0.05$, $R^2= 33.54\%$; *F. sylvatica*: $F_{2,29}= 13.54$, $P \leq 0.01$, $R^2=48.29\%$) (Figure 4.14b). Another species that showed changes in the proportion of records under its

dominant host was *I. rimosa.* The species has become commoner under *F. sylvatica* ($F_{1,37}$= 5.55, P≤0.05) however, there was no significant relation detected in another common hosts to suggest that the species was shifting its host.

Unlike other genera, *Lactarius* sp. showed no trend of relations between the proportions of fruiting records under different hosts over time (Figure 4.15). The proportions of records of several Lactarius sp. were almost unchanged under their dominant hosts (e.g. *L. torminosus, L. turpis* and *L. vellerus*) over years suggesting that these species showed no responses of either host expansion or host shift.

For the genus *Russula*, 25% of the species have shown significant changes in the proportion of fruiting records under their dominant host. This includes *R. atropurpurea* (Figure 4.16c), *R. cyanoxantha* (Figure 4.16e), *R. delica* (Figure 4.16f) and *R. virescens* (Figure 4.16o). *R. atropurpurea* has been found under seven hosts since its first record in the 1951 (Figure 4.5c). *Q. robur* was the dominant host for *R. atropurpurea* and the fungus seems to have become commoner under this tree since the 1980s (Figure 4.16c). Meanwhile, *R. cyanoxantha* (Figure 4.16e) and *R. delica* (Figure 4.16f) showed declines under their commonest host, *Q. robur*, over time. Among the two species, only *R. delica* showed a significant increase under its other common host, *F. sylvatica* (*Q. robur*: $F_{1,23}$= , P ≤ 0.05, R^2= 18.78% ; *F. sylvatica*: $F_{1,23}$= 4.96 , P ≤ 0.05, R^2= 17.73%) (Figure 4.17). Two significant relations were also found in *R. virescens* where the species has become commoner under its dominant host, *Q. robur* (Figure 4.16o) while getting rarer under its second most common host, *F. sylvatica* (*Q. robur*: $F_{1,24}$= 25.85, P≤0.01 , R^2= 51.85%; *F. sylvatica*: $F_{2,23}$= , P≤0.01 , R^2= 33.35%) (Figure 4.18). There were no trends found in the other *Russula* sp.

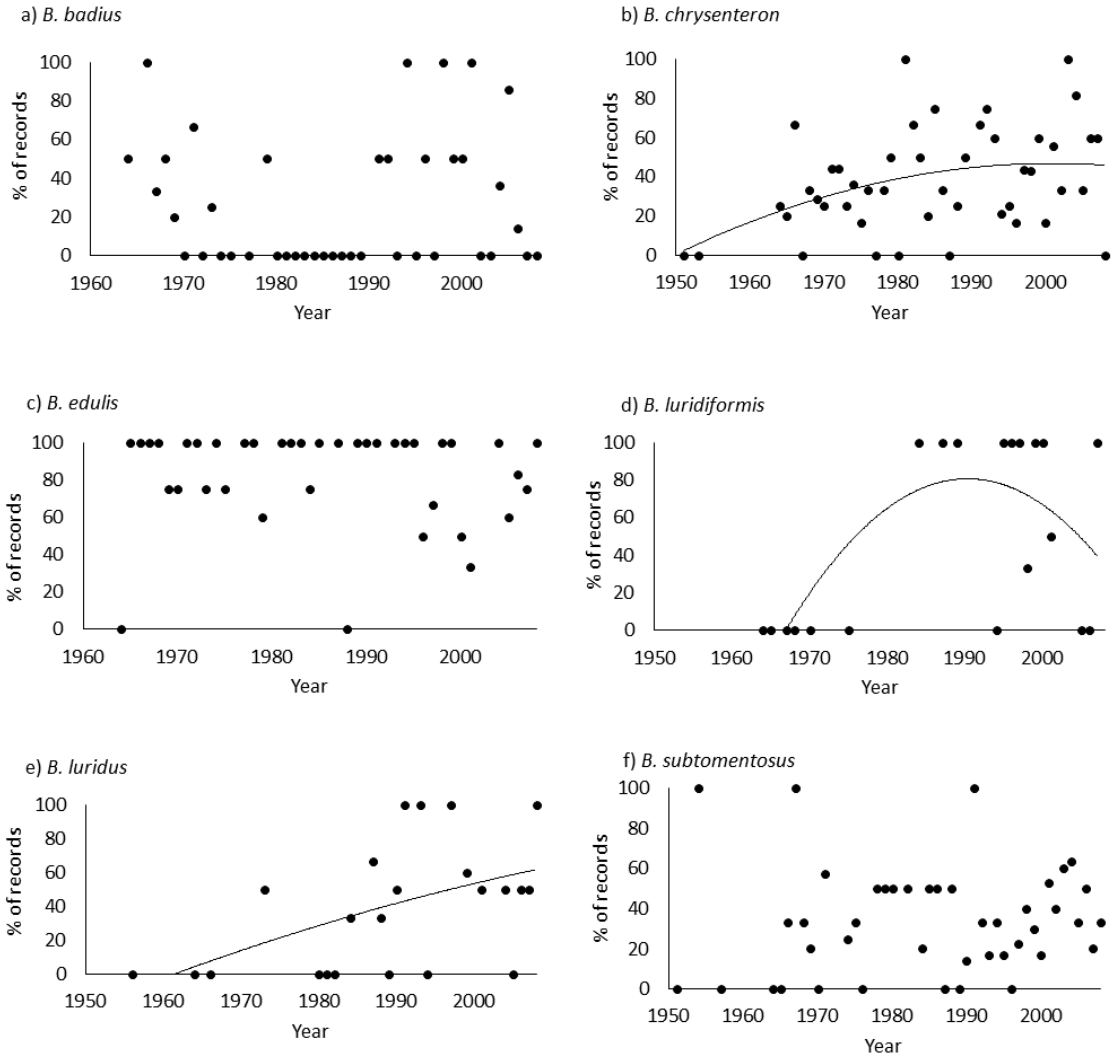


Figure 4.12(a-f) The proportion of fruiting records for each *Boletus* sp. found under their dominant host. a) *B. badius* (Host: *P. sylvestris*), b) *B. chrysenteron* (Host: *Q. robur*), c) *B. edulis* (Host: *Q. robur*), d) *B. luridiformis* (Host: *F. sylvatica*), e) *B. luridus* (Host: *F. sylvatica*) and f) *B. subtomentosus* (Host: *Q. robur*). The trend lines indicate significant changes in the proportions of records over time.

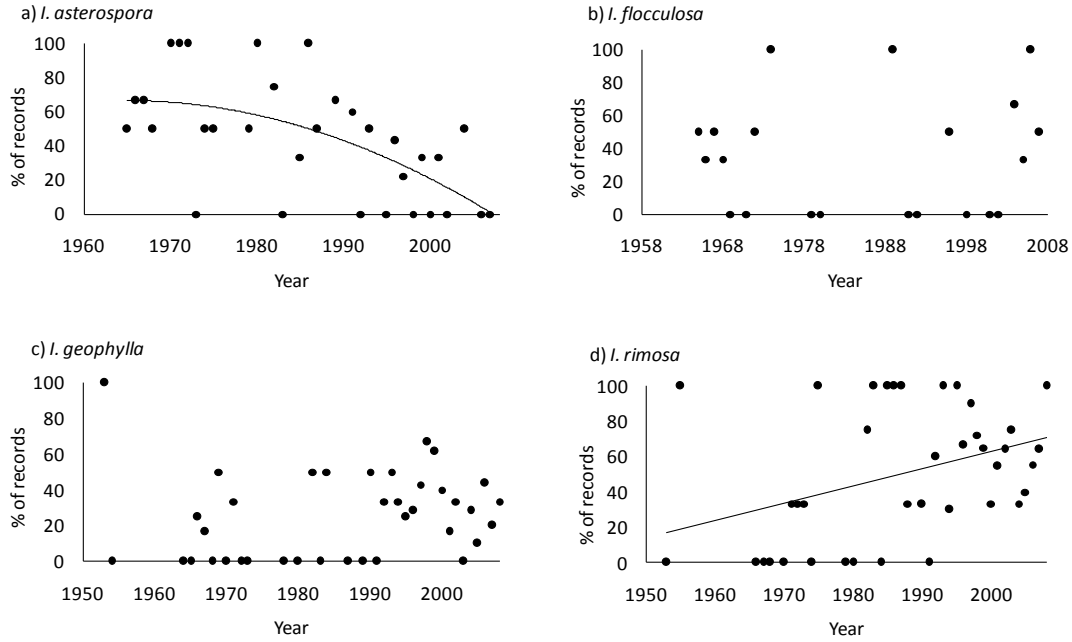


Figure 4.13(a-d) The proportion of fruiting records for each *Inocybe* sp. found under their dominant host. a) *I. asterospora* (Host: *Q. robur*), b) *I. flocculosa* (Host: *Q. robur*), c) *I. geophylla* (Host: *F. sylvatica*) and d) *I. rimosa* (Host: *F. sylvatica*). The trend lines indicate significant changes in the proportions of records over time.

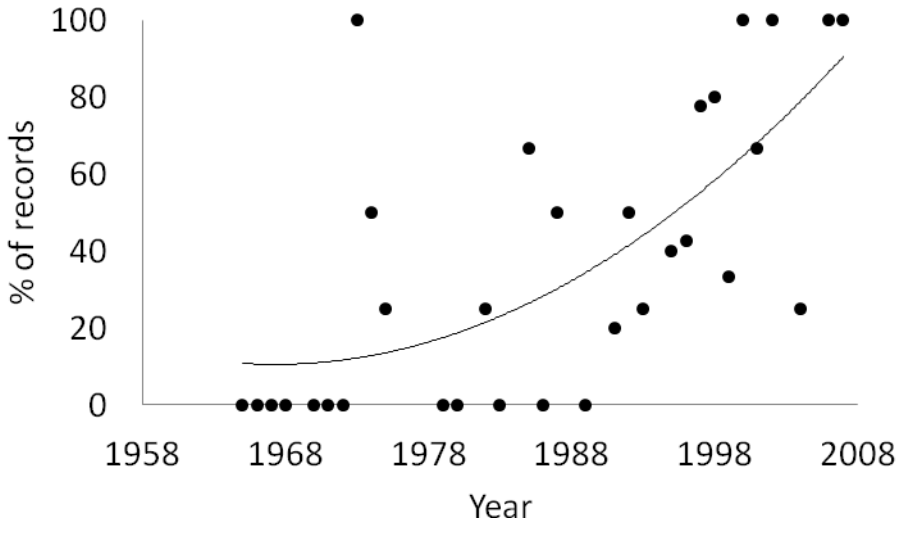


Figure 4.14 The proportion of fruiting records for *I. asterospora* found in each year under *F. sylvatica*.

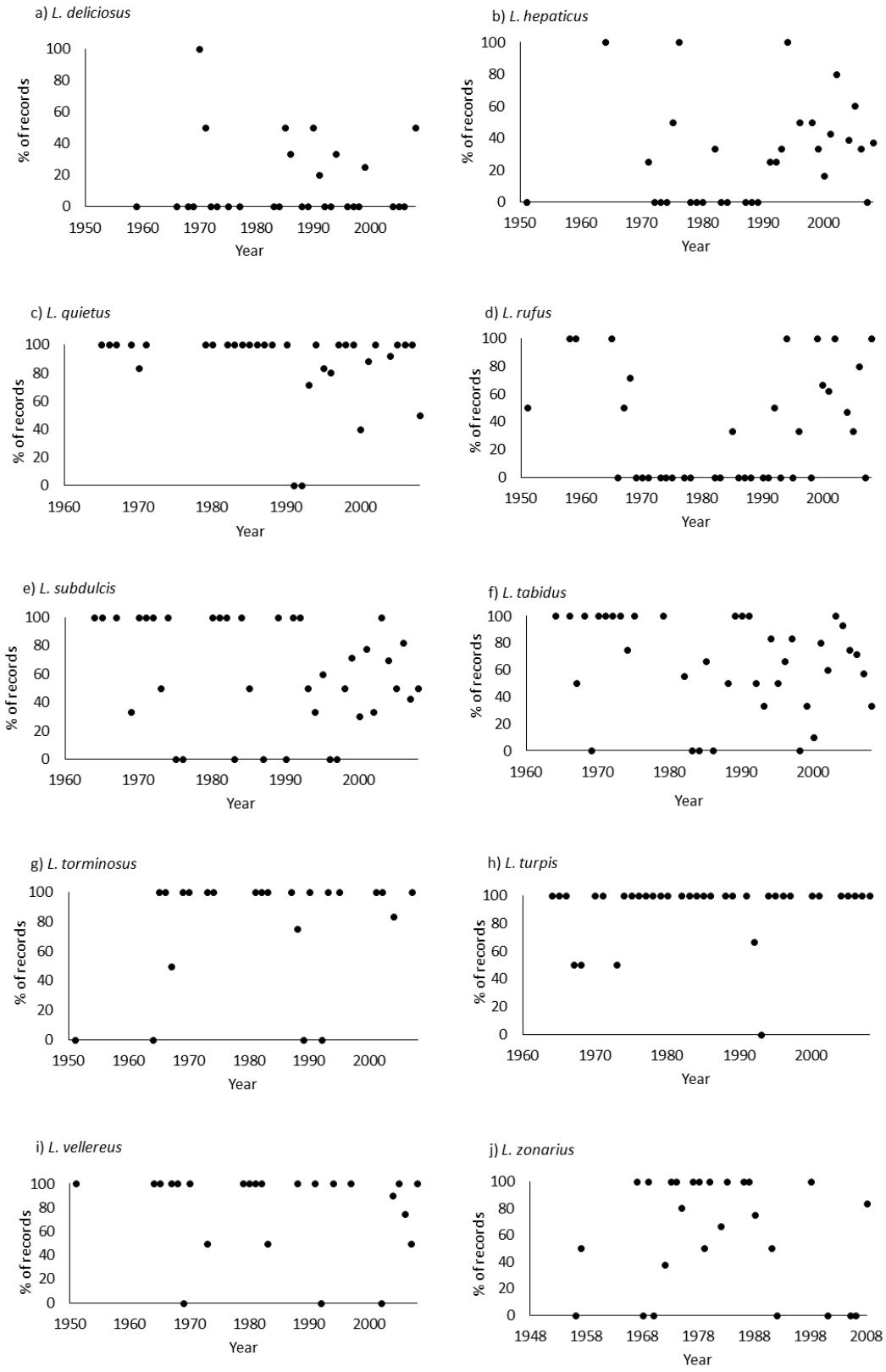


Figure 4.15(a-j) The proportion of fruiting records for each *Lactarius* sp. found under their dominant host. a) *L. deliciosus* (Host: *P. sylvestris*), b) *L. hepaticus* (Host: *P. sylvestris*), c) *L. quietus* (Host: *Q. robur*), d) *L. rufus* (Host: *P. sylvestris*), e) *L. subdulcis* (Host: *Q. robur*), f) *L. tabidus* (Host: *Q. robur*), g) *L. torminosus* (Host: *B. pendula*), h) *L. turpis* (Host: *B. pendula*), i) *L. vellereus* (Host: *Q. robur*) and j) *L. zonarius* (Host: *F. sylvatica*).

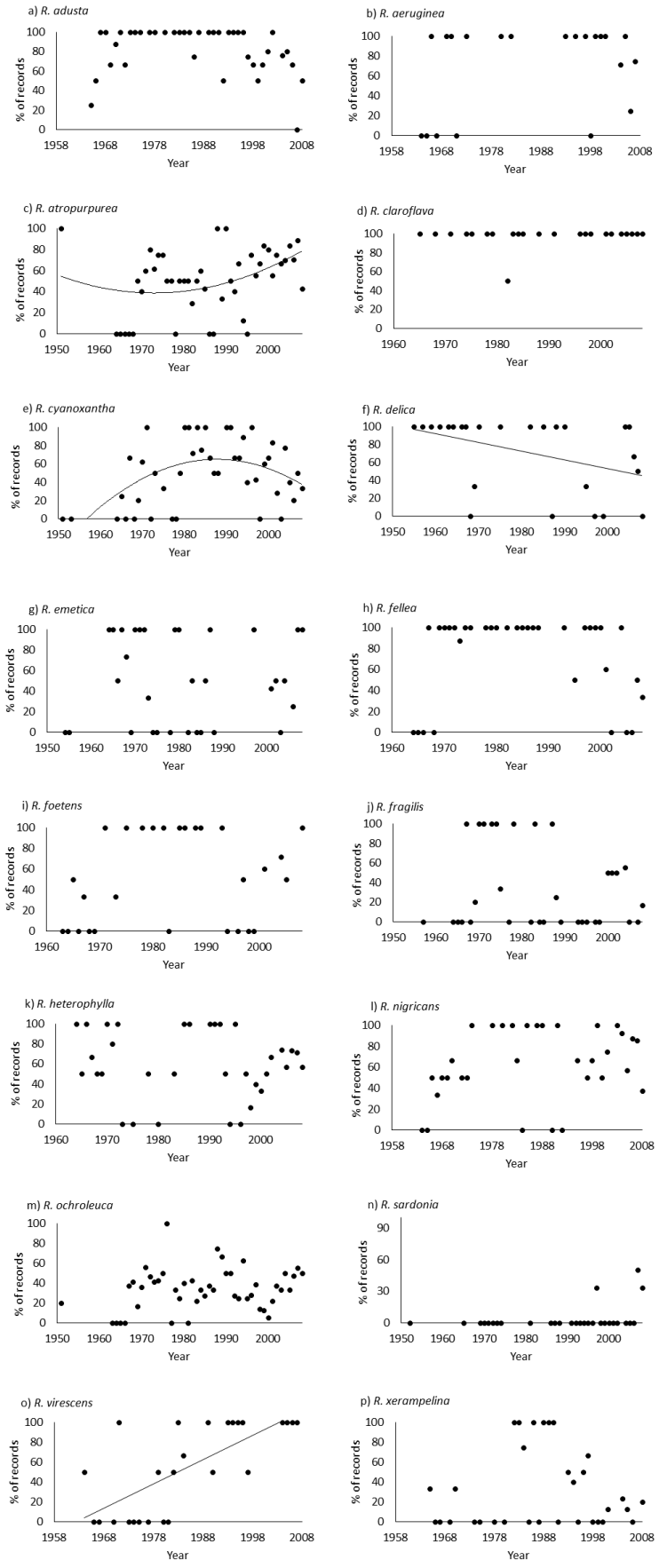


Figure 4.16 (a-o) The proportion of fruiting records for each *Russula sp.* found under their dominant host. a) *R. adusta* (Host: *Q. robur*), b) *R. aeruginea* (Host: *B. pendula*), c) *R. atropurpurea* (Host: *Q. robur*), d) *R. claroflava* (Host: *B. pendula*), e) *R. cyanoxantha* (Host: *Q. robur*), f) *R. delica* (Host: *Q. robur*), g) *R. emetica* (Host: *P. sylvestris*), h) *R. fellea* (Host: *F. sylvatica*), i) *R. foetens* (Host: *Q. robur*), j) *R. fragilis* (Host: *Q. robur*), k) *R. heterophylla* (Host: *Q. robur*), l) *R. nigricans* (Host: *Q. robur*), m)*R. ochroleuca* (Host: *Q. robur*), n) *R. sardonia* (Host: *Q. robur*) and o) *R. virescens* (Host: *Q. robur*). The trend lines indicate significant changes in the proportions of records over time.

In general, analysis of mycorrhizal associates with their hosts showed that there were a number of mycorrhizal species showed dramatic host shifts in their fungal-host association. Analysis showed that most shifts involved the movement from *Q. robur* to *F. sylvatica*, shown by *A. vaginata, I. asterospora, R. delica* and *R. virescens*. Meanwhile, *A. fulva* appeared to shift from *B. pendula* to *Q. robur* (Table 4.3). More than 50% of the total species in three genera namely *Boletus, Inocybe* and *Russula* have displayed host expansion in their fungal-host associations (Table 4.2). *Lactarius* showed the highest percentage of species to have shifts in their host association (100%) followed by genus *Boletus* (67%) and *Russula* (56%). Fewer shifts were recorded in the mycorrhizal genera *Amanita, Inocybe* and *Russula*.

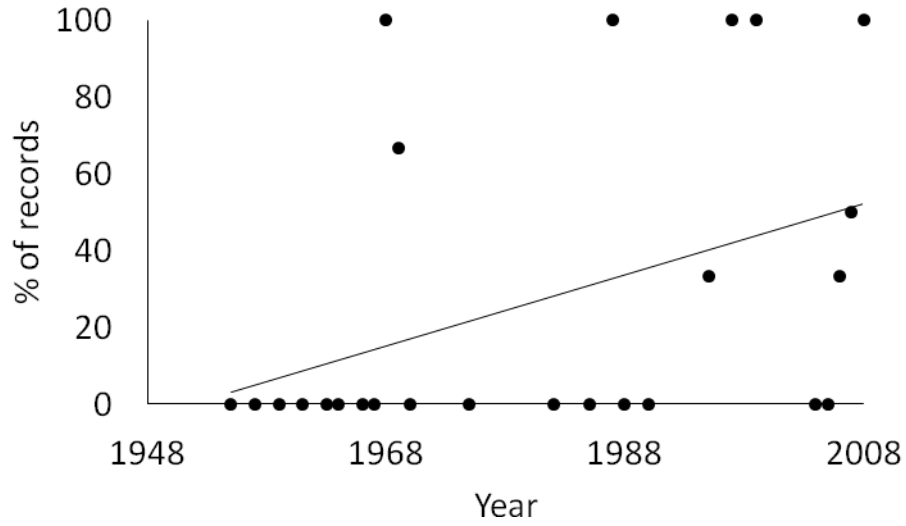


Figure 4.17 The proportion of fruiting records for *R. delica* found in each year under *F. sylvatica*.

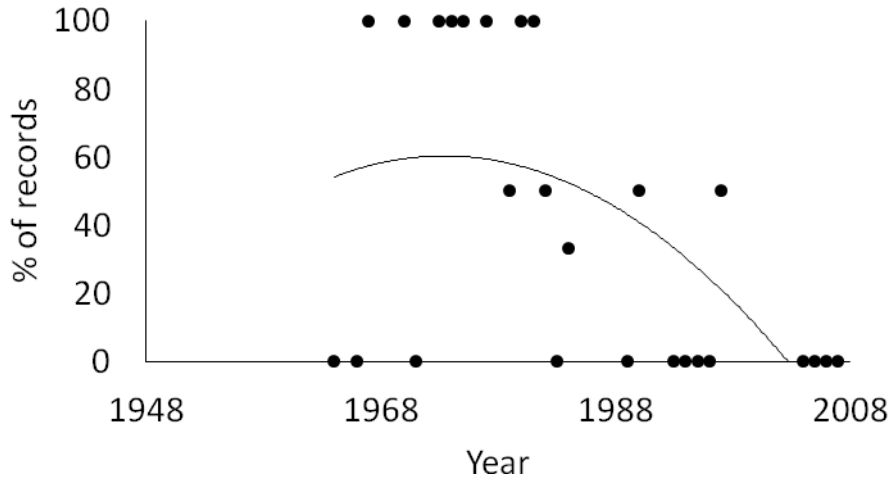


Figure 4.18 The proportion of fruiting records for *R. virescens* found in each year under *F. sylvatica.*

Table 4.3 Response of mycorrhizal species showing host shift.

Host shift			No. of mycorrhizal species
Q. robur	→	*F. sylvatica*	4
F. sylvatica	→	*Q. robur*	0
Q. robur	→	*B. pendula*	0
B. pendula	→	*Q. robur*	1

Table 4.4 Responses of mycorrhizal genera in the study. (*n* represents number of species) (% represents percentage of species from the total sp. in the genus).

	Expansion (*n*)(%)	**Shift (*n*)(%)**	**No response (*n*)(%)**	**Both expand & shift**
Amanita sp.	4 (44.4)	2 (22.2)	3 (33.3)	0
Boletus sp.	4 (67)	0	2 (33)	0
Inocybe sp.	3 (75)	0	0	1 (25)
Lactarius sp.	3 (30)	0	7 (70)	0
Russula sp.	9 (56)	2 (13)	5 (31)	0

4.3.2.2 Saprotrophic genera

Clitocybe, *Collybia* and *Mycena* were the genera that were grouped into saprotrophic fungi in the study. In *Clitocybe*, most of its species have shown significant changes in the proportion of fruiting records found under their dominant host (Figure 4.19). These species were *C. brumalis* (Figure 4.19a), *C. fragrans* (Figure 4.19b), *C. gibba* (Figure 4.19d), *C. nebularis* (Figure 4.19e), *C. phyllophila* (Figure 4.19f) and *C. vibecina* (Figure 4.19h). Among the six species, *C. fragrans* seemed to show a decreased pattern until the year 2000, thereafter increasing again beneath its commonesthost, *Q. robur,* from 2000 onwards. Meanwhile, *C. fragrans* was found to be significantly commoner under its second most common host, *F. sylvatica* in the 1980s but started to decrease in the beginning of 1990s (Figure 4.20). Both host records for *Q. robur* and *F. sylvatica* were best fitted to a second order polynomial with time compared to a linear function (*Q.robur*: $F_{2,26}$= 10.69, P≤0.01, R^2=45%; *F. sylvatica*: $F_{2,26}$=4.69, P≤0.05, R^2=27%). Another *Clitocybe* sp. that showed significant relations in its dominant host and its next common trees was *C. gibba*. This species has been found under a total of 12 hosts since mid-1960s (Figure 4.6d) and has become commoner under *F. sylvatica* (Figure 4.19d). However, the species was later found less commonly under *Q. robur* (*F. sylvatica*: $F_{2,36}$= 10.73, P ≤ 0.01, R^2 = 37% ; *Q. robur*: $F_{2,36}$= 10.81 , P ≤ 0.0 , R^2= 38%) (Figure 4.21).

There has also been a significant trend in the proportion of records of certain species in the genus *Collybia* beneath their commonest trees, including *C. confluens* (Figure 4.22b), *C. dryophila* (Figure 4.22c) and *C. peronata* (Figure 4.22f). *C. confluens* was first recorded in 1963 and since then this species has been found under 8 hosts (Figure 4.7b) and has become commoner under *F.* sylvatica. Meanwhile, *C. confluens* has become rarer under its second commonest host, (*Q. robur*) suggesting shifts between the two most common hosts (*F. sylvatica*: $F_{2,34}$=8.44, P ≤ 0.01, R^2= 33% ; *Q. robur*: $F_{2,34}$=19.62, P ≤ 0.01, R^2= 54%) (Figure 4.23). On the other hand, *C. dryophila* has become rarer under its most common host, *Q. robur.* This species has been recorded under 13 hosts since 1956 (Figure 4.7c) and over time, it has been commonly found

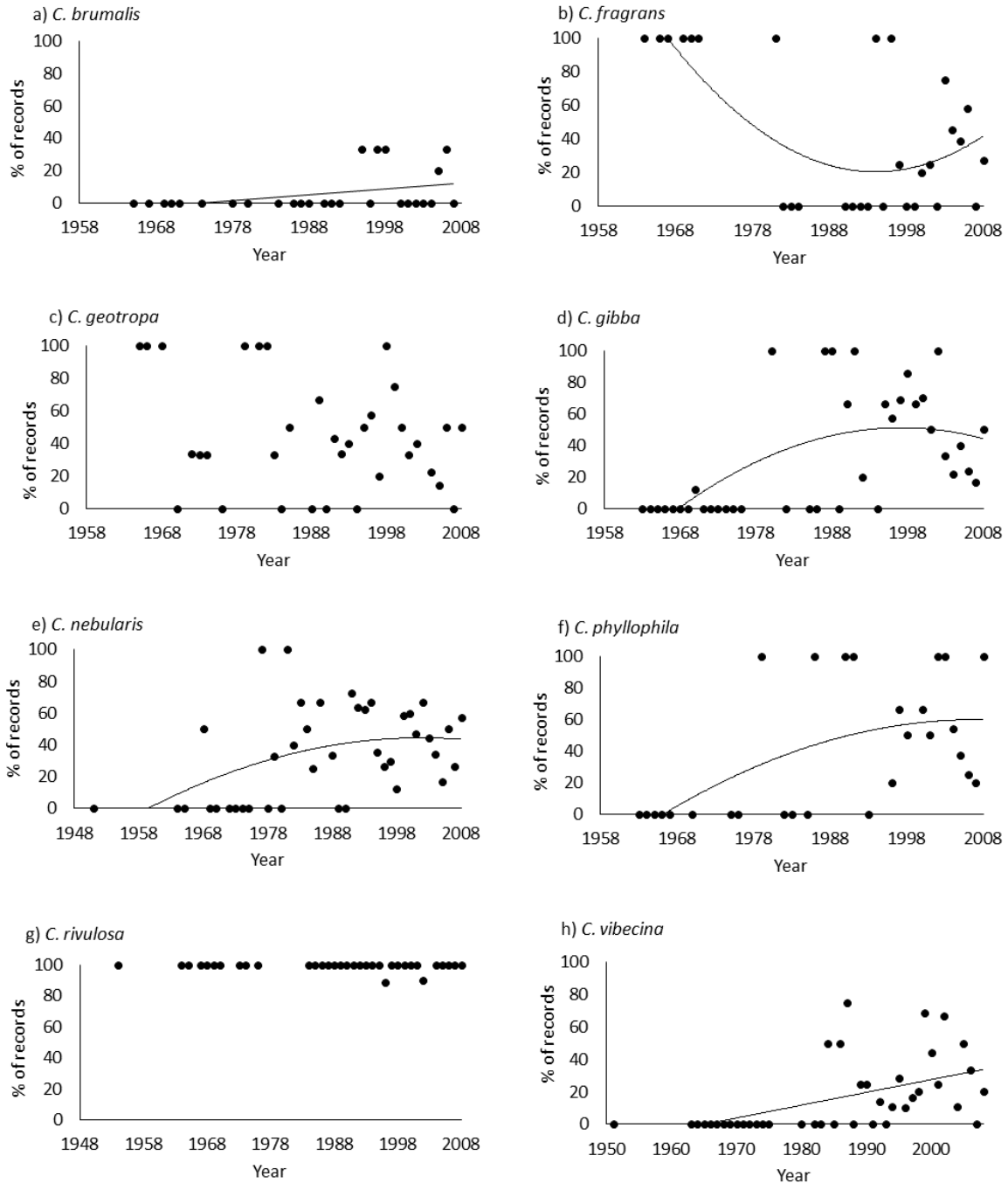


Figure 4.19(a-h) The proportion of fruiting records for each *Clitocybe* sp. found under their dominant host. a)*C. brumalis* (Host: *F. sylvatica*), b) *C. fragrans* (Host: *Q. robur*), c) *C. geotropa* (Host: *F. sylvatica*), d) *C. gibba* (Host: *F. sylvatica*), e) *C. nebularis* (Host: *F. sylvatica*), f) *C. phyllophila* (Host: *F. sylvatica*), g) *C. rivulosa* (Host: grass) and h) *C. vibecina* (Host: *F. sylvatica*). The trend lines indicate significant changes in the proportions of records over time.

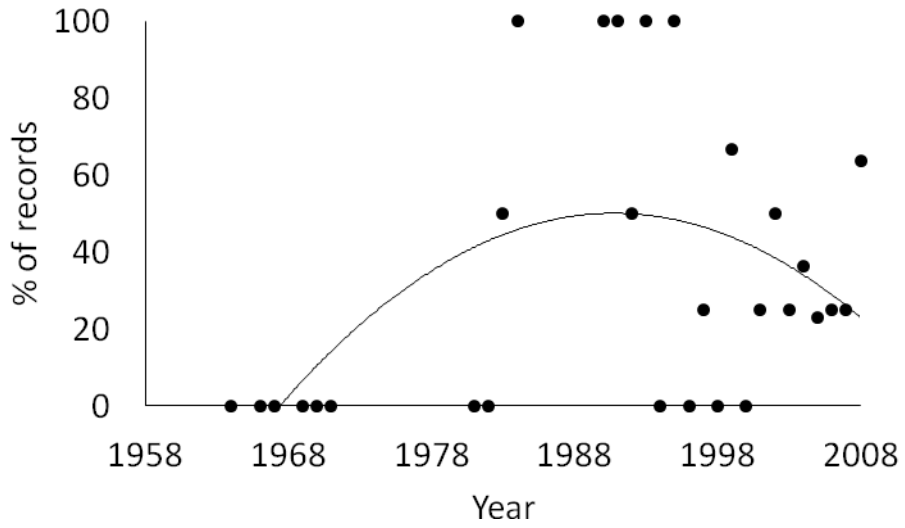


Figure 4.20 The proportion of fruiting records for *C. fragrans* found in each year under *F. sylvatica.*

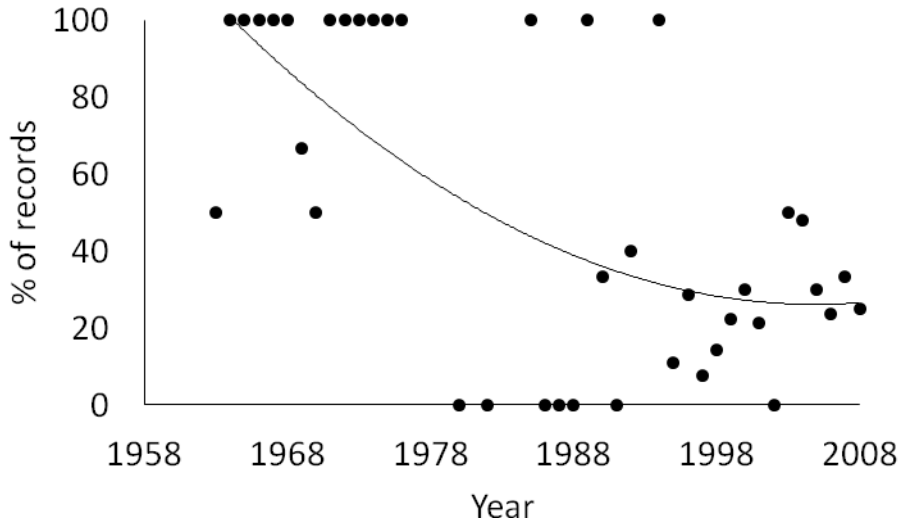


Figure 4.21 The proportion of fruiting records for *C. gibba* found in each year under *Q. robur.*

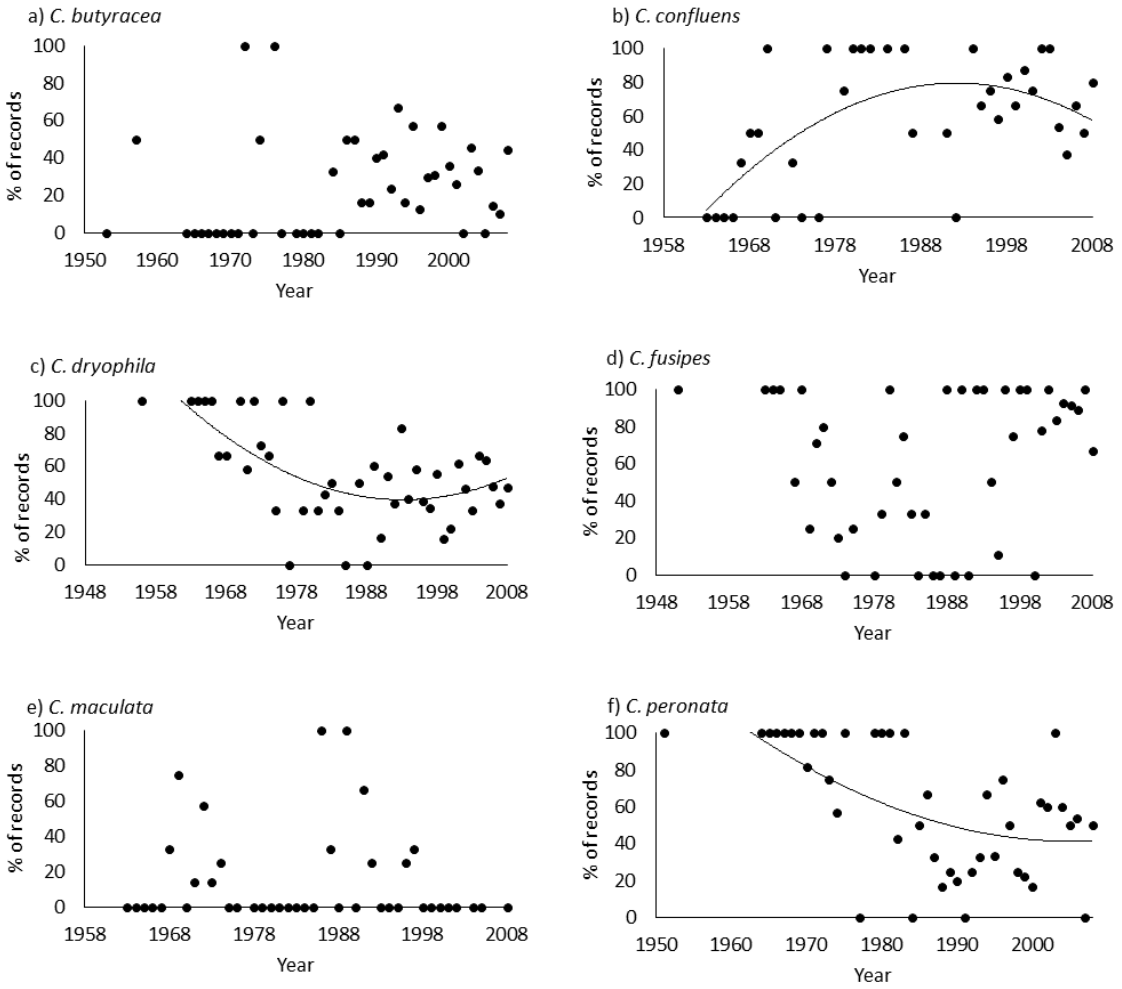


Figure 4.22 (a-f) The proportion of fruiting records for each *Collybia* sp. found under their dominant host. a)*C. butyracea* (Host: *F. sylvatica*), b) *C. confluens* (Host: *F. sylvatica*), c) *C. dryophila* (Host: *Q. robur*), d) *C. fusipes* (Host: *Q. robur*), e) *C. maculata* (Host: *F. sylvatica*) and f) *C. peronata* (Host: *Q. robur*). The trend lines indicate significant changes in the proportions of records over time.

under *F. sylvatica* (*Q.robur*: $F_{2,41}$=15.07, $P \leq 0.01$, R^2= 42% ; *F. sylvatica*: $F_{2,41}$=10.17, $P \leq 0.01$, R^2= 33%) (Figure 4.24). A similar trend was also found in *C. peronata* where the species has become less common under its dominant host, *Q. robur* but more common under the second common host, *F. sylvatica.* (*Q. robur*: $F_{2,41}$=11.79, $P \leq 0.01$, R^2= 37%; *F. sylvatica*: $F_{2,41}$=10.76, $P \leq 0.01$, R^2= 34%) (Figure 4.25).

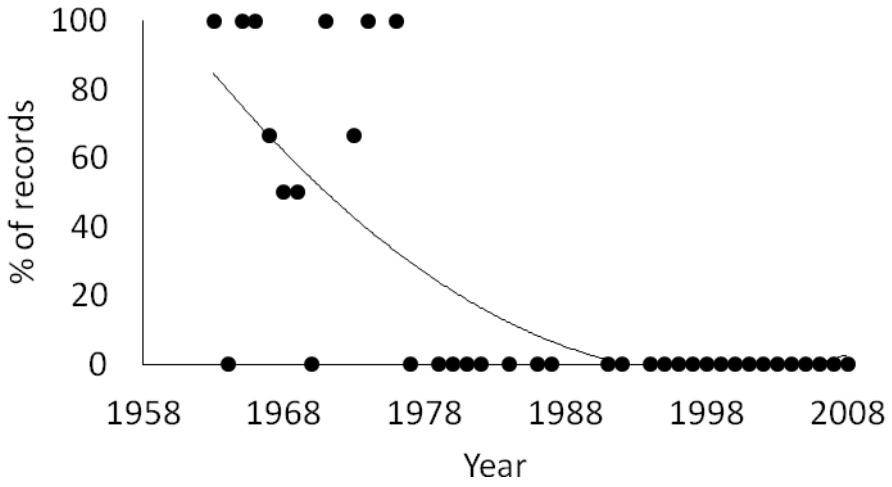


Figure 4.23 The proportion of fruiting records for *C. confluens* found in each year under *Q. robur.*

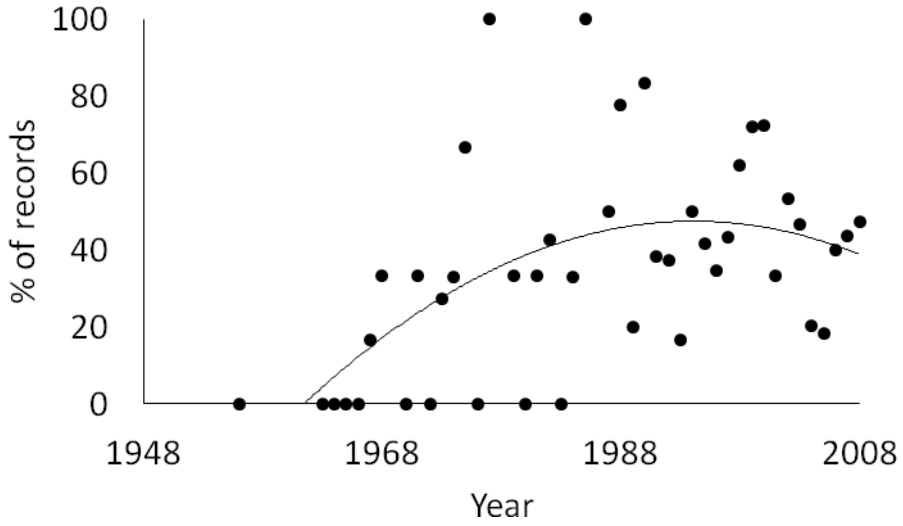


Figure 4.24 The proportion of fruiting records for *C. dryophila* found in each year under *F. sylvatica.*

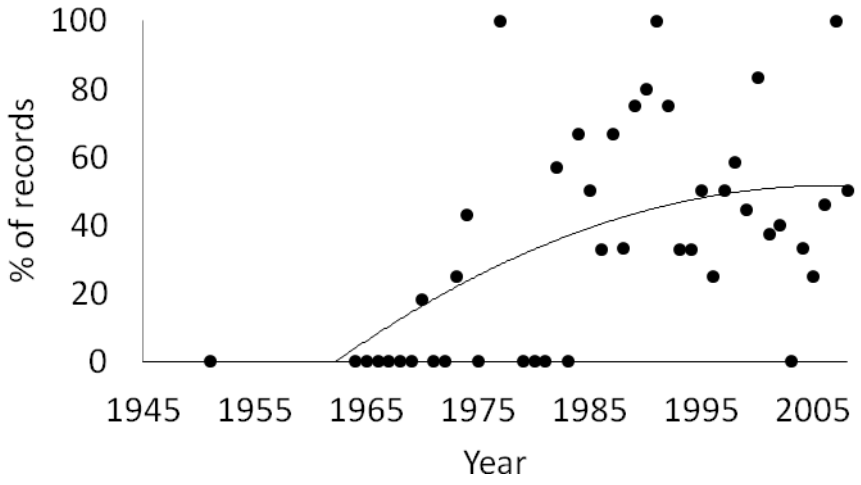


Figure 4.25 The proportion of fruiting records for *C. peronata* found in each year under *F. sylvatica.*

In the genus *Mycena*, 56% of the species have shown a significant trend in the proportion of records found under their commonest host. Overall, most species with significant change showed an increase in the fruiting records under their main host over time, indicating that these species have tended to become commoner under this tree. The species involved were *M. adscendens* (Host: *F. sylvatica*) (Figure 4.26a), *M. capillarys* (Host: *F. sylvatica*) (Figure 4.26c), *M. filopes* (Host: *F. sylvatica*) (Figure 4.26e), *M. pura* (Host: *F. sylvatica*) (Figure 4.26h), *M. galopus var. nigra* (Host: *F. sylvatica*) (Figure 4.26i), *M. hiemalis* (Host: *F. sylvatica*) (Figure 4.26k), *M. leptocephala* (Host: *P. sylvestris*) (Figure 4.26m), *M. luteoalba* (Host: grass), *M. olida* (Host: *F. sylvatica*) (Figure 4.26p) and *M. polygramma* (Host: *F. sylvatica*) (Figure 4.26r). Of all these species, only *M. luteoalba* showed a decreasing number of records in its dominant host, grass (Figure 4.26n). Cumulatively, this species has been found under four hosts (Figure 4.26) over 44 years of records. Above all, most *Mycena* sp. did not show any significant relations between their main host and the other common hosts for each of the species except for *M. olida*. This species was commonly found under two trees namely *F. sylvatica* and *Q. robur* in the first 30 years of recording, however, later years have shown that *M. olida* tend to increase under *C. avellana* (*F. sylvatica*:

$F_{2,17}$= 6.63, P ≤ 0.01 , R^2=44%, *Q. robur*: $F_{2,17}$=4.40 , P ≤ 0.05 , R^2=0.05 , *C. avellana*: $F_{2,17}$=3.52 , P ≤ 0.05, R^2=29%) (Figure 4.27).

There were a number of saprotroph species that showed dramatic host shifts in their fungal-host association. The majority of the shifts involved movement from *Q. robur* to *F. sylvatica*, shown by *C. fragrans, C. dryophila* and *C. peronata*. Meanwhile, two species, *C. gibba* and *C. confluens* have shown shifts from *F.* sylvatica to *Q. robur*. There was only one species that displayed a shift from *F. sylvatica* to *C. avellana* and that was *M. olida* (Table 4.3).

All three genera, *Clitocybe, Collybia* and *Mycena* have shown over 50% of species showing host expansion in their fungal-host associations (Table 4.6). *Clitocybe* showed the highest percentage of species to have shifts in their host association (88%) followed by *Collybia* (83.3%) and *Mycena* (77.8%). On the other hand, fewer species were found to have shifted host from the most common to the less common hosts (Table 4.5).

If we compare the summaries in Table 4.4 and Table 4.6, then we find that 84% of saprotrophic species appeared to have shown an expansion in their host association, while only 53% of mycorrhizal species have done so. This difference is significant (χ^2 = 8.5, d.f. =1, p < 0.01).

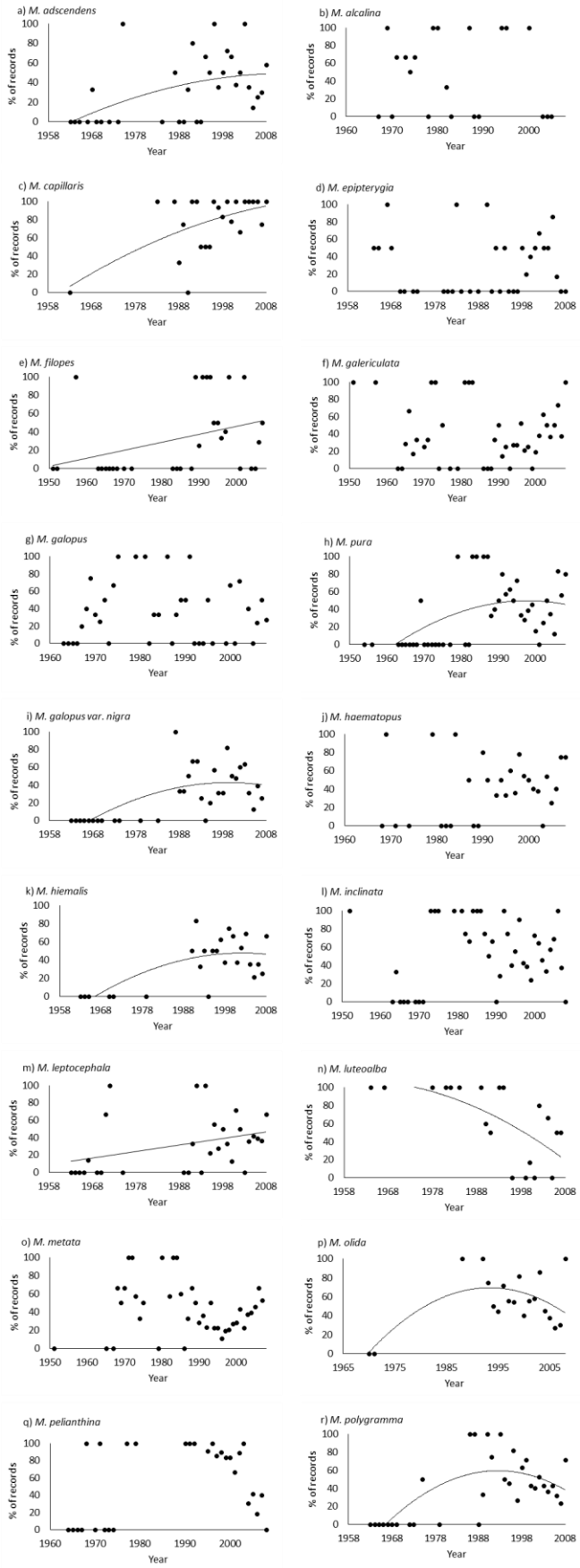
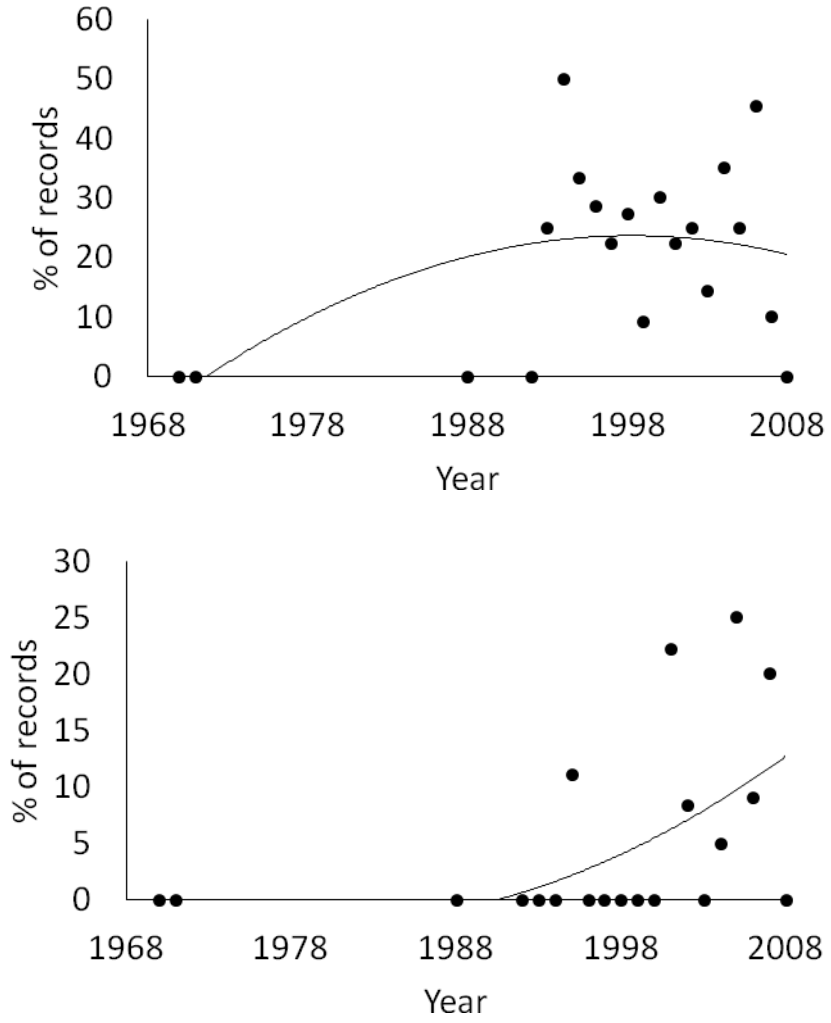


Figure 4.26(a-r) The proportion of fruiting records for each Mycena sp. found under their dominant host. a) M. adscendens (Host: F. sylvatica), b) M. alcalina (Host: F. sylvatica), c) M. capillaries (Host: F. sylvatica), d) M. epipterygia (Host: P. sylvestris), e) M. filopes (Host: F. sylvatica), f) M. galericulata (Host: Q. robur), g) M. galopus (Host: F. sylvatica), h) M. pura (Host: F. sylvatica), i) M. galopus var. nigra (Host: F. sylvatica), j) M. haematopus (Host: F. sylvatica), k) M. hiemalis (Host: F. sylvatica), l) M. inclinata (Host: Q. robur), m) M. leptocephala (Host: P. sylvestris), n) M. luteoalba (Host: grass), o) M. metata (Host: Q. robur), p) M. olida (Host: F. sylvatica), q) M. pelianthina (Host: F. sylvatica) and r) M. polygramma (Host: F. sylvatica). The trend lines indicate significant changes in the proportions of records over time.



F**igure 4.27** The proportion of fruiting records for *M. olida* found in each year under a) *Q. robur* and b) *C. avellana*.

Table 4.5 Responses of saprotrophic species showing host shifts.

Host shift			No. of saprotrophic species
Q. robur	→	*F. sylvatica*	3
F. sylvatica	→	*Q. robur*	2
F. sylvatica	→	*C. avellana*	1
C. avel	→	*F. sylvatica*	0

Table 4.6 Summary of responses of saprotrophic genera in the study. (*n* represents number of species)) (% represents percentage of species from the total sp. in the genus).

	Expansion (*n*)(%)	**Shift (*n*)(%)**	**No response (*n*)(5)**	**Both expand & shift**
Clitocybe sp.	7(88)	0	1(13)	2
Collybia sp.	5(83.3)	0	1(16.7)	3
Mycena sp.	14(77.8)	1(5.6)	3(16.7)	0

4.4 Discussion

Analysis of this 58 y fruiting data set has indicated that: (i) fungal host range measured by the rate of accumulation of hosts over time is different between the functional groups, (ii) saprotrophic fungi were more likely to show host range expansion and host shift in comparison to mycorrhizal fungi, (iii) there were higher tendencies of both saprotrophic and mycorrhizal species to shift host especially from *Q. robur* to the other host plants.

In any normal sampling regime, as the sampling effort increases, more species tend to be found up to a certain point, where the rate of discovery of new species will decline and so the accumulation curve should gradually stop rising (Henderson 2003). This pattern is extremely common in birds (e.g. Rosenzweig 1995), insects (e.g. Arriaga *et al.* 2012; Hamel-Leigue 2012), mammals (e.g. Mugerwa *et al.* 2012), reptiles (e.g. Sung *et al.* 2012) and even in fish studies (e.g. Cousins & Priedel 2012). Most fungal studies also show a similar pattern, where species richness appears to rise with increasing sampling effort (da Silva *et al.* 2012; Piepenbring *et al.* 2012; Phosri *et al.* 2012). However, analysis of the species accumulation curves in this study showed that several species have shown a completely different response from the classic pattern of accumulation in both mycorrhizas and saprotrophic groups. This suggests that over the course of time, sampling was insufficient to reach stability and immediately suggests that if more years were to be taken , further host species would be found and the line will still rising. However, results of host expansion are scattered among genera in this study which would suggest that expansion in hosts indicated real biological changes

rather than sampling artefacts. The biological changes may include the inherent individual characteristics of each fungal species, space availability, dispersal and combative interactions between fungi.

The saprotrophic group has shown greater host range expansion compared to the mycorrhizal group. This group that contained wood-decay fungi and leaf litter decomposers, and obtain their source of nutrients by utilizing dead organic materials in the form of plant debris and leaf litter. Robinson *et al.* (2005) showed that the decomposer fungal community is structured strongly by several mechanisms that include substrate availability (e.g. dead wood, plant debris), substrate quality and a certain degree of 'host' specificity (or host exclusivity) in the community (Zhou and Hyde 2001). Meanwhile, Ellis & Ellis (1997) found that the decomposer fungal community is structured by different types of fungi; host-specific fungi, species that are more widespread and also species that live upon several hosts (plurivorous fungi).

Mycorrhizas, on the other hand, are intimately associated with long-lived trees and have been reported to involve 10,000 fungal species and 8,000 plant species globally (Taylor & Alexander 2005; Finlay 2008). In terms of theirs function in the environment, mycorrhizal fungi are known to have an intimate relationship (symbiotic) with their host plants. In this context, a mycorrhizal fungus gains a carbon supply and other essential organic substances from the tree and in return, the plant benefits from receiving water and nutrient resources to grow. The close ties between ectomycorrhizal fungi (ECM) and their plant hosts would lead us to expect greater host fidelity i.e. less host expansion, and indeed was found in this study. This fact is supported by Robinson *et al.* (2005) who explained that the structure and composition of fungal assemblages in mycorrhizas is mostly affected by host specificity. For example, Newton & Haigh (1998) in their studies of host specificity in ectomycorrhizal fungi in the UK have found out that almost half of the total host information collected appeared to be specific to a single host plant species.

The studies on fungi and their responses of host expansion using long term datasets are still lacking and to my knowledge, this study is the first to compare host expansion of common species of mycorrhiza and saprotrophs. Gange *et al.* (2011) applied a similar method to examine an expansion of host range for *Auricularia-auricula judae*, however no comparison between mycorrhiza and saprotrophic species was conducted in their study. Meanwhile, Hall *et al.* (1998) have reviewed various hosts that associated with *B. edulis*. This species has been found with several hosts including *Abies* sp. (Fir), *Castanea* sp., *Castanopsis* sp. (Chinquapin), *Fagus* sp., *Keteleeria* sp. (Asian conifer), *Lithocarpus* sp. (Stone oak), *Pinus* sp., *Picea* sp., *Quercus* sp. and *Tsuga* sp. (Hemlock) suggesting that it tends to associate with different hosts in different locations. Besides that, the authors also found that *B. edulis* has been commonly found within other species such as *A. muscaria* and *A. rubescens* in several countries e.g. China, England, New Zealand, France and Austria. They predicted that the three species may have similar ecological requirements or other biological associations between them, as these species were also found to fruit at similar times of the year.

Additionally, the results of the host range analysis were found to be closely correlated with changes in the phenological aspects from the previous Chapter 3. For the genus *Amanita*, all species that have expanded their host range tend to display an expansion in their length of fruiting. Meanwhile, in *Inocybe,* the majority of species with expanded host range have shown later FFD and LFD in their phenological analyses. Meanwhile, species that showed host expansion in the genus *Lactarius* and *Russula* displayed earlier fruiting and showed expansion in their length of fruiting. For the saprotrophic genera, all species that showed host expansion in the genera *Clitocybe*, *Collybia* and *Mycena* tend to show longer fruiting seasons across the 58 years.

Unlike host expansion, only a few species in both the mycorrhizal and saprotrophic groups have shifted from their former host to the other host plant. The least number of species with shifted host was predicted from mycorrhizal group due to their nature of being faithful to their host plants. However, some movement was still seen among these species, therefore, there must be external elements in the environment that trigger the ability of the fungus to shift its host. Pringle *et al.* (2009), who have

conducted molecular tests on the collections of European and American *A. phalloides* not only discovered the rate of spread of the species in California, they also found out that the species in the North America seems to have shifted hosts from *Pinus strobus* to the coast live oak *Q. agrifolia* (Arora 1986; Wolfe & Pringle, unpublished; Pringle *et al*. 2009). Mycorrhizal fungi are known to acquire nutrients in the soil in many ways that include extending the plant root systems to places where nutrient supplies are abundant. Besides that, the ability of mycorrhizal species to produce hyphal structures called rhizomorphs have enabled the efficient transfer of nutrients from the point the nutrients are taken to their host plant roots. Finally, mycorrhizal fungi have a high surface-to-volume ratio compared to plants and therefore increase the nutrient absorption rates better than its host (Allen 1991). Any changes to those biological functions could have influenced the shifting of a mycorrhizal species to another host for its survival.

Changes in the biology of host plants may have contributed to this change too. However one factor that can be discounted is changes in the frequency of occurrence of the host trees in this study. Virtually all the fungal records in the data base are from the New Forest, which comprised of plantation or ancient woodlands. While there may have been the occasional tree death in these woodlands, they have not changed greatly in their composition over the course of the study (E.G. Gange, personal communication). Instead, climate change has been one of the key elements that can influence such things as the effects of increasing temperature have been monitored on many floral species over a long period of time. Plant phenology which is defined as the timing of natural event that include the events of bud burst, annual flowering and stem elongation were found to show changes over the time. Long term studies have shown similar trends where most events in plant phenology have been accelerated which has resulted in the extension of plant's growing season productivity (Grace, 1988; Saxe *et al.* 2001; Badeck *et al.* 2004; Vitasse *et al.* 2009; Richardson *et al.* 2010; Gunderson *et al.* 2012). Autumn is now delayed in the UK causing delay to leaf colouring and leaf fall (e.g. Sparks & Gill 2002), this could also alter its mutual partner;

mycorrhizal community structure and affect leaf litter saprotrophs that also rely on the forest litter for growth function, diversity and distribution.

Meanwhile, most host shifts in the saprotrophic species were found to coincide exactly with their trends in their host expansion. There has been no specific explanation for the outcomes of such interaction, thus it is impossible to be certain if any factor has been the key to the host expansion and host shift in these species. However, changes of abiotic factors in an environment such as temperature, rainfall, humidity or soil condition could have influenced which host a fungus prefers to establish upon as these elements have demonstrated strong influences on the formation of fruit bodies (Wasterlund & Ingelog 1981; Vogt *et al.* 1981; Dighton & Mason 1985; Ruehling & Tyler 1990; Straatsma *et al*. 2001). Other factors that may affect changes in fungal-host associations include the quality of soil organic matter. Straatsma *et al.* (2001) suggested that a shift in the amount of substrate for saprotrophic species may be an indication of the accumulation of soil organic matter which partly derived from atmospheric gases (e.g. nitrogen, CO_2).

Meanwhile, all fungal species that shifted their hosts also showed significant changes in their fruiting phenology. For example, *A. fulva* has shown an earlier FFD and later LFD which caused the length of fruiting to expand significantly. Similar trends were also shown by *C. gibba, C. dryophila* and *M. olida.* Another trend was displayed by *A. vaginata* that showed earlier FFD and LFD which consequently shortened the fruiting season for this species. Meanwhile, *I. asterospora* showed later FFD and LFD without a significant change in its length of fruiting. Among 16 *Russula* sp., only *R. virescens* and *R. delica* displayed host shift in their fungal-host associations. Phenologically, these two species displayed later FFD and restricted length of fruiting season. For *C. fragrans*, other than the ability to shift its host, this species also showed earlier appearance and tended to have an expanded length of fruiting. Finally, two *Collybia* sp. that also shifted their host tended to show similar phenological changes; later LFD and an expansion in their length of fruiting.

During the period of study, the majority of fungal species that once grew under *Q. robur* were found growing on the other host plants. Species that show such changes

were *A. vaginata, I. asterospora, R. delica, C. fragrans, C.dryophila* and *C. peronata.* These species were more likely to be found under *F. sylvatica* than *Q. robur* in later years. One of the possible explanations for this shift would be due to the declining number of oak. Oak decline phenomenon would be another problem faced by *Quercus* sp. and has been recorded in many European countries including the British region since the past thirty years (Thomas *et al.* 2002). Similar authors have summarised that the symptoms of the oak decline include 1) crown thinning in the upper canopy; 2) remaining leaves arranged in tufts at the end of the shoots; 3) discolouration or yellowing of the leaves; 4) reduced leaf size; 5) epicormic shoots; 6) slime flux on the trunk; 7) premature death of tree bark and 8) reductions in diameter growth. The decline was firstly recorded in 1739-1748 and was seen in North-eastern Germany. There were assumptions that oak declines in Central European countries were triggered by the following biotic and abiotic factors: insect defoliation combined with either winter frosts, summer drought or flooding and followed by infections from pathogenic fungi (e.g. *Armillaria, Agrilus*) (Thomas *et al.* 2002). Thus while the actual quantity of oak trees in the study has probably not changed, it is possible that their quality as hosts for the fungi have. Besides that, changes in atmospheric pollutants, levels of nitrogen deposition and soil chemistry that have happened in the UK over the last 20 years (Matejko *et al.* 2009) coupled with changes in plants and animal communities (Morecroft *et al.* 2009) also could have been potential factors that may affect the population dynamics and physiology of trees such as *Q. robur* leading to the alteration of host preference of a fungus.

In this study, the genus *Lactarius* has shown an unexpected, and to some extent surprising result where none of the species within the genus have shown any response of host shift. Also, in terms of host expansion, most *Lactarius* did not show progressive trends either. Members of this genus have been reported in ectomycorrhizal association with many trees and shrubs (Nuytinck *et al.* 2004). On top of that, their important ecological role as late-stage root colonizers in a range of ectotrophic plant communities is well documented (Hutchinson 1999; Nuytinck *et al.* 2004). Melin (1953) in his review has quoted the author Romell (1939) who presented evidence that the

mycorrhizal fungi that include *Lactarius* sp. are only able to produce fruit bodies when these species are living in connection with their host partners. He also suggested that these mycorrhizal fungi are able to absorb soluble carbohydrates from their host roots which therefore made these species as an active parasite on their host trees. In nature, *Lactarius* sp. especially *L. vellereus,* has developed mechanisms of sharp taste and its apparent resistance to attack by predators such as insect and snails. The internal compounds responsible for these mechanisms were isovelleral and velleral which are part of the chemical defence system for the fungus when it is attacked by predators (Sterner *et al.* 1985). Therefore, these mechanisms, to some extent could increase the survival rate of *Lactarius* sp. as different fungal species may associate with one single host tree in the forest. The genus *Lactarius* is one of the larger genera of ectomycorrhizal Basidiomycota with about 400 species identified worldwide (Nuytinck *et al.* 2004).

Host specificity is a well-known term to mycologists that is usually based on observations of fruit body occurrence (Watling 1984; Newton 1998). This term was defined by Newton (1991) as the 'preference' of fungi for particular host trees and has been the key factor to determine ECM diversity. However, patterns of host-specificity in both ECM and saprotrophic fungi are still lacking in the literature. No definite fact has been said about whether mycorrhiza and saprotrophic species belong to either 'species with restricted host range' or 'species with broader host range' groups. Nevertheless, several findings from phytological studies may be able to resolve this issue. Newton & Haigh (1998) in their analysis found that there was a high proportion of ECM species in Britain which are apparently specific to a single host genus. Furthermore, the authors also did not deny that mycorrhizal associations with their hosts are widespread in nature. This is also supported by Molina *et al*. (1992) who described the fruit bodies of mycorrhizal genera such as *Leccinum, Suillus, Rhizopogon* and *Hydnangium* are 80 - 100% restricted to individual plant genera or families.

Unlike mycorrhizas, most studies on saprotrophic species have shown a much greater degree of width in their host preference. Leaf litter agarics have rarely shown strong host specificity in respect of broad classes of hosts such as monocotyledonous versus

dicotyledonous plants in the tropics, or gymnosperms versus angiosperms in temperate forests (Hedger, 1985; Lodge 1993,1997; Watling, 1995). Different patterns are seen in the larger-sized of ascomycetous fungi that belong to the family *Xylariaceae* (e.g. *Xylaria polymorpha*). These fungi are very frequently restricted to fruit on leaves and fruits of particular host plant genera or families in the tropics (Laessøe & Lodge 1994). Meanwhile, Gonzalez & Rogers (1989) have similarly found that there was a high proportion of the *Xylaria* species in Mexico to be host-specific.

Understanding fungal-host associations are as important as the conservation of rare species as well as habitat management (Lonsdale *et al.* 2008; Gange *et al.* 2011). The fact that this study has shown that fungi have the ability to expand and/or shift their host, suggests that this may cause risks in terms of the conservation status of fungi, especially the rarer species. Since this study has been the first attempt to look for changes in fungal-host associations using long-term dataset, it would beneficial to have further investigations on to what extent the environmental factors discussed could change fungal-host associations in forest ecosystems.

4.5. Host shifts in fungi caused by climate change?

Note: This part of the chapter has been published as Gange AC, Gange EG, Mohammad AB, Boddy L. 2011. Host shifts in fungi caused by climate change? *Fungal Ecology* **4**(2): 184-190.

4.5.1 Introduction

The degrees of host specificity among fungi are varied; some tend to have narrow host ranges (e.g. pathogens, endophytes and mycorrhiza) meanwhile others (e.g. saprotrophs) exhibit broader degrees of host selectivity (Zhou & Hyde 2001). Selectivity of particular habitat types is widespread amongst wood decay fungi, ranging from tropical wetlands and mangrove forest to temperate deciduous and boreal forest (Boddy 2001; Gilbert & Sousa 2002; Boddy & Heilmann-Clausen 2008; Gilbert *et al.* 2008; Gange *et al.* 2011). Determination of host selectivity is often based on the appearance of fruit bodies on particular substrates, however, when considering associations based on the occurrence of fruit bodies, it is worth remembering that these may not always have a directional basis (Rayner *et al.* 1985). Furthermore, it may sometimes be that the associated organism provides a suitable base, perhaps sometimes related to specific physical or chemical stimulation, upon which fruiting is facilitated (Rayner *et al*. 1985). Nevertheless, the absence of fruit bodies in substrates does not necessarily indicate absence of mycelia (Gange *et al.* 2011), as fungi require sufficient resources to start fruiting, with different species having different needs for fruiting (Boddy 2001).

Factors that trigger the host selectivity of wood decay fungi are complex and include wood microclimate, rate of dying host, gaseous regime and temperature (Boddy 2001). Besides that, intimate interactions between several wood decay fungi and their substrates that develop in sapwood after a period of latency may also contribute to selectivity (Boddy 2001). In addition, environmental factors (e.g. moisture, irradiation, temperature, salinity) that determine the distributions of vulnerable plants could be one of the triggering factors to host selectivity (Gilbert *et al.* 2008).

Many mycologists have applied the analysis of species richness and species diversity in order to get an understanding about fungal communities in the ecosystem. The estimation of fungal species richness can be obtained in two ways; 1) using accumulation curves followed by statistical models (e.g. Unterseher *et al.* 2008) or 2) using tree species richness in order to predict fungal species richness (Unterseher *et al.* 2008) and both methods were proven to have been successfully applied to wood decay fungi by Unterseher *et al.* (2008). Nevertheless, to date, no studies have applied these techniques to the host range of wood decay fungi.

Another aspect that is still lacking in information is whether fungi change their host ranges over time. In order to obtain pure results of changes in fungal host range, these involve the separation of sampling effect from real biological changes (Gange *et al*. 2011). To achieve this, a long-term data set that contains a list of fruit body records and tree species is required. To date, such datasets are extremely rare except by Gange *et al.* (2007) that contains over 60,000 fungal records gathered over a 58 y period within a 30 km radius of Salisbury, Wiltshire, UK. The present study involved analyses of fungal fruiting on the woody plant *Sambucus nigra* (elder) over 59 y and also focused on the host range of the common fungus *Auricularia auricula-judae*, a species that is often cited as being mostly confined to this host. Using methods similar to Unterseher *et al.* (2008), the total number of hosts with which fruit bodies of the fungus may be associated were estimated.

4.5.2 Methods and analysis

The data set used in the study was previously analysed by Gange *et al.* (2007), with additional records of sporocarps from the period 2006 – 2008, giving a total of 59 y of records. More details on the background of the dataset can be found in Chapter 2 of this thesis.

There were 238 records of fungi fruiting on *S. nigra* in the dataset. *A. auricula-judae* was one of the species seen to grow upon this tree. In total, there were 308 records of

A. auricula-judae in the dataset, which was found in 47 of the 59 y. The total number of hosts per year on which *A. auricula-judae* was found was calculated and the cumulative number of hosts where the species occurred was plotted as a species accumulation curve. Meanwhile, the non-parametric Chao2 index was used to estimate the total number of hosts upon which is this species might be found. The software package used for this analysis was Species Diversity and Richness 4.1.2 (Pisces Conservation Ltd, Lymington). The cumulative number of fungal species that were found on *S. nigra* was also calculated and the total number of fungi that likely to be found upon this host tree was also calculated using a similar method.

Finally, possible changes in host associations (i.e. host expansion and host shift) over time between *S. nigra* and its associated fungal species were also examined. The proportion of records of *A. auricula-judae* that was found on different hosts in each year was also calculated. A similar method was also applied to the other common species on *S. nigra*, which was *Hyphodontia sambuci* (Elder Whitewash).

4.5.3 Results

There was a weak linear trend of increasing foray number through time ($F_{1,57} = 5.4$, $P \leq 0.05$) (Figure 4.28a). Years such as 1955, 1959, 1961, 1976 and 2002 have shown fewer forays due to low rainfall in the late summer/early autumnal months in these years. Therefore, no fruit bodies were found at certain times in these years and have resulted to an absence of records and forays. Meanwhile, sampling effort has been constant over time ($F_{1,56} = 2.666$. $P < 0.001$; $R^2 = 97.9\%$), indicated by the almost linear trend in the cumulative number of sites (Figure 4.28b).

The first fruiting date (FFD) of *A. auricula-judae* has become significantly earlier in the year ($t = -3.3$, $P < 0.01$) (Figure 4.29a). Early records show that the mean FFD for the species was day 332 (Nov. 28th) ± 6.7 d, while the in the current decade, the mean FFD has been day 257 (Sep. 14th) ± 12.3 d. Meanwhile, last fruiting date (LFD) has been

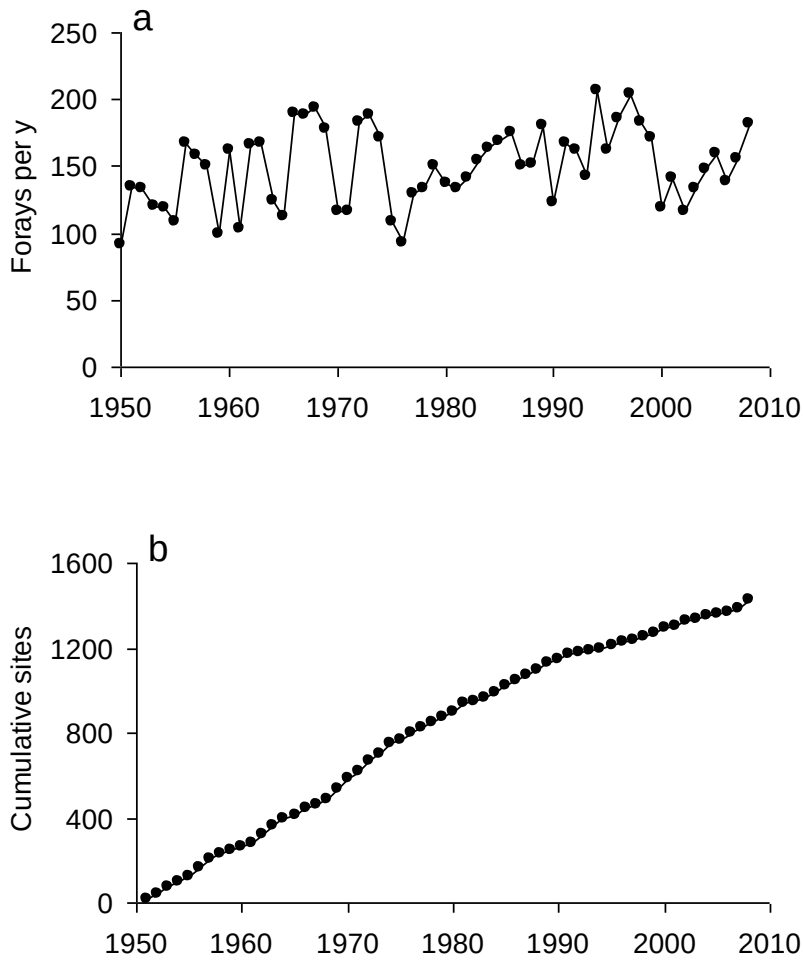


Figure 4.28 a) The total number of forays per year and b) the cumulative number of sites sampled over the 58 y study.

unchanged (Figure 2b). Since there was an earlier trend of fruiting for *A. auricula-judae*, this has led to an expansion of the fruiting season for this species (t = 3.5, P < 0.01). Additionally, in the 1950s, the fruiting season was on average 37.4 ± 2.5 d, while in the current decade it has expanded to 95.4 ± 15.2 d. FFD was negatively relatedto the earlier average March temperature ($F_{1,45}$ = 7.04, P < 0.05), that displayed a significant warming trend over the time period ($F_{1,56}$ = 5.3, P <0.05) (Figure 4.29). As a result, *A. auricula-judae* fruits earlier when March temperature is higher over years. There was no significant relationship between rainfall and FFD and LFD although rainfall patterns have also changed across years, with July and August getting drier (P = 0.051, P = 0.055), while October has started to become significantly wetter now than in the 1950s.

There has been a significant change in the number of hosts per year on which *A. auricularia-judae* was found upon over years and this change has become apparent since the end of the 1970s (Figure 4.30a). These data are best fitted by a polynomial

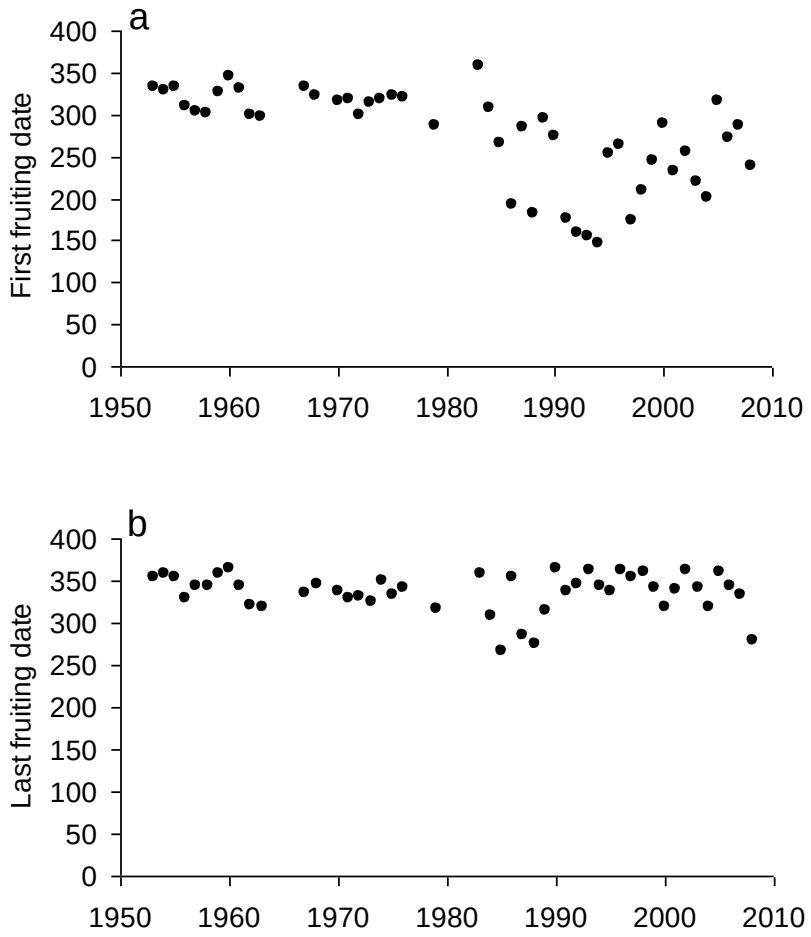


Figure 4.29 First fruiting date (a) and last fruiting date (b), expressed as Julian day, of *A. auricula-judae* from 1950 – 2008.

($F_{5,41}$ = 16.9, $P \leq 0.001$; R^2 = 67.3%). Besides that, the cumulative number of hosts upon which the species has been found also shows an exponential increase since the 1970s (Figure 4.30b) and the total estimated number of hosts using the Chao2 index is 32.67 ≈ 33. The species was firstly recorded in 1953 and was only found upon a single host, *S. nigra* for two decades. The first year in which the species was found on the host other than *S. nigra* was 1979 and this was *Fagus sylvatica.* To date, the species has been found on 16 hosts (Table 4.7).

The number of fungi found fruiting on *S. nigra* has shown a steady increase since the 1990s (Figure 4.30c; Table 4.8). In total, 12 species have been found to fruit on elder. Nevertheless, the Chao2 index that used to estimate total species richness in this host indicates 21.7 ≈ 22 suggesting that the total observed is less than the real value.

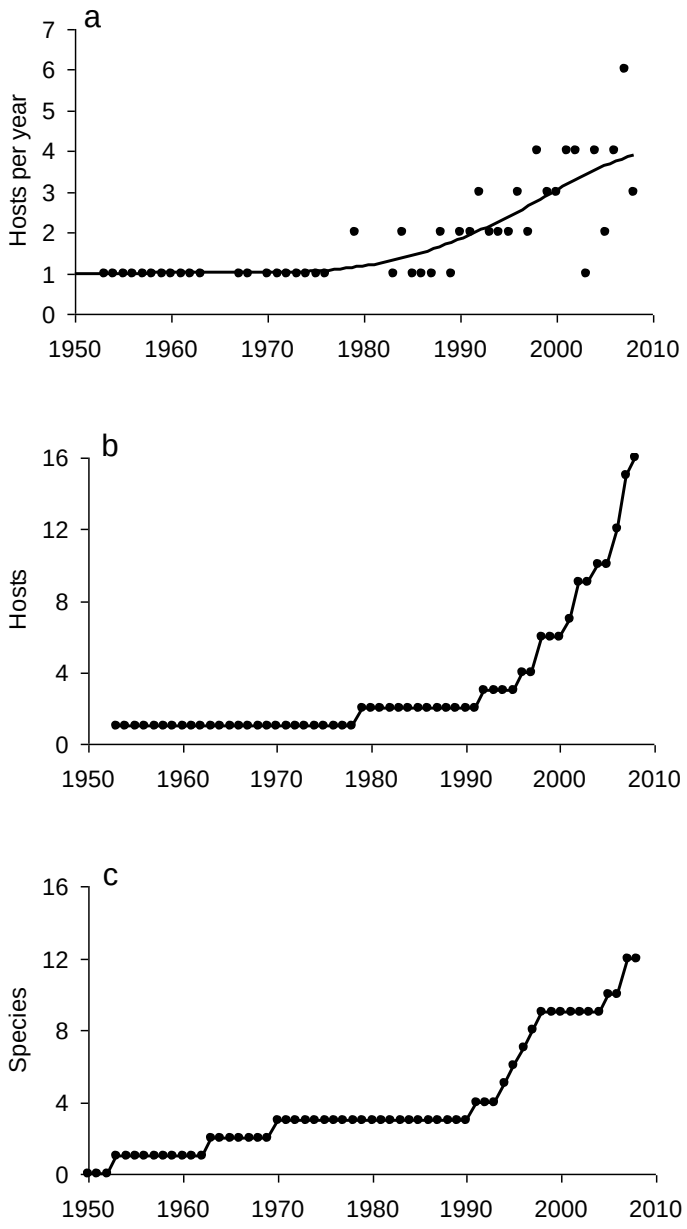


Figure 4.30 a) The number of hosts per year upon which *A. auricula-judae* was recorded, b) the cumulative number of hosts for this fungus and c) the cumulative number of fungal species found fruiting upon dead wood of *S. nigra*.

Table 4.7 Hosts of *A. auricula-judae*, with first year of observation.

Host	First year seen
Sambucus nigra	1953
Fagus sylvatica	1979
Populus nigra	1992
Fraxinus excelsior	1996
Euonymus europaeus	1998
Quercus robur	1998
Ulmus procera	2001
Acer pseudoplatanus	2002
Salix alba	2002
Prunus laurocerasus	2004
Ailanthus altissima	2006
Betula pendula	2006
Alnus glutinosa	2007
Corylus avellana	2007
Elaeagnus x ebbingei	2007
Buddleia davidii	2008

There has been a dramatic fall in the proportion of fruiting records of *A. auricula-judae* on *S. nigra* (Figure 4.31a) indicating that the species more or less has shifted its host to another species, especially *F. sylvatica* (Figure 4.31b). This change in host association appears to have happened since the late 1970s, which is also coincidental with the change in fruiting phenology (Figure 4.29). This fact is supported by records on *S. nigra* and *F. sylvatica* (Figure 4.31a,b) that displayed a second order polynomial when regressed against time, and which provided a much better fit than a linear function (*S. nigra* : $F_{2,44}$ = 75.03, P <0.001, R^2 = 77.3%; *F. sylvatica*: $F_{2,44}$ = 37.03, P < 0.001, R^2 = 62.7%).

The second most common species in the dataset that fruits on *S. nigra* is *Hyphodontia sambuci*. This species was found in 36 y of the study but showed no significant change in its FFD over time ($F_{2,33}$ = 0.33, P > 0.05). Besides *S. nigra* (70%), *H. sambuci* has been

recorded from three other hosts namely *F. sylvatica* (28%), *Ilex aquifolium* (1%) and *Clematis vitalba* (1%). There were no changes on the number of hosts per year (Figure 5A) and also on the proportion of records each year on *S. nigra* (Figure 4.32).

Table 4.8 Fungi found on *Sambucus nigra*, with first year of observation

Fungal species	First year seen
Auricularia auricula-judae	1953
Hyphodontia sambuci	1979
Crepidotus cesatii	1992
Armillaria mellea	1996
Myceina speira	1998
Flammulina velutipes	1998
Dothidea sambuci	2001
Collybia erythropus	2002
Polyporus squamosus	2002
Basidiodendron cinereum	2004
Inonotus cuticularis	2006
Sarcoscypha austriaca	2006

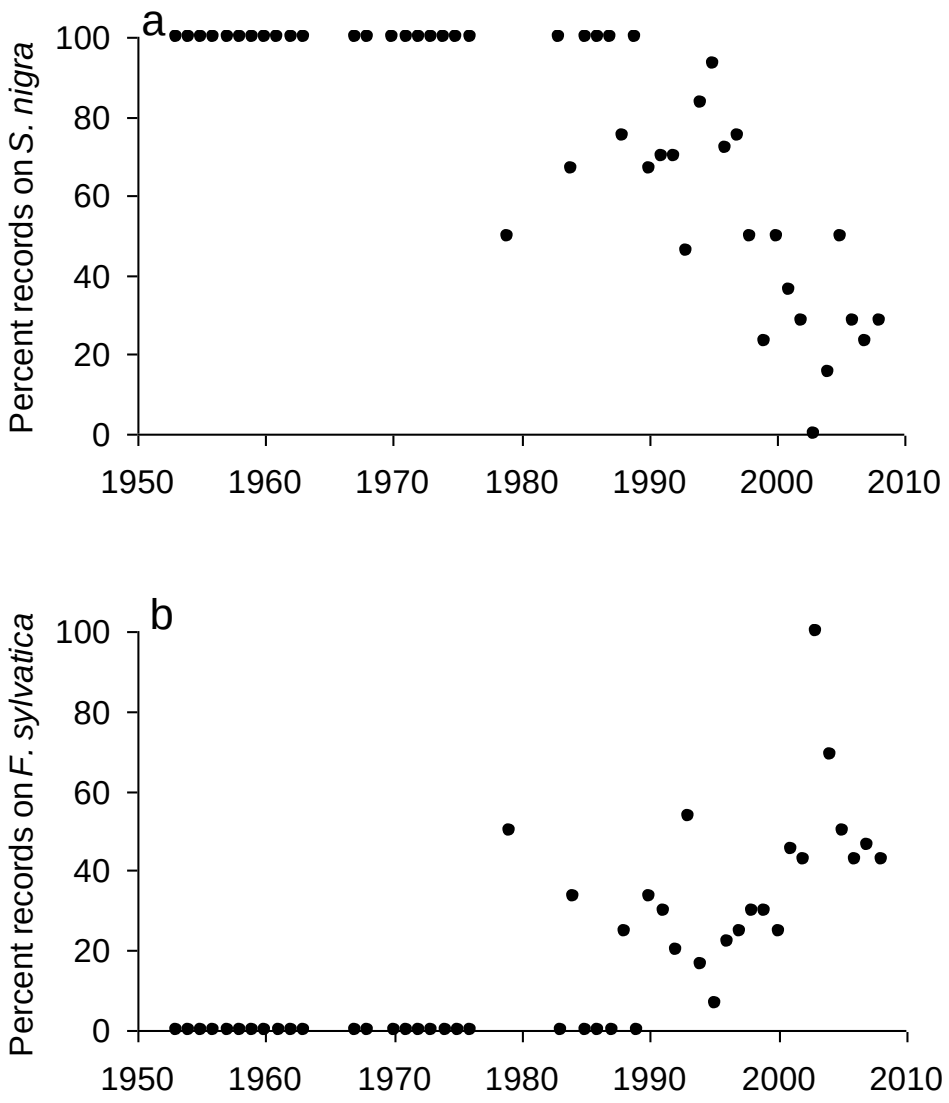


Figure 4.31 The proportion of fruiting records for *A. auricula-judae* in each year that were found on a) *Sambucus nigra* and b) *Fagus sylvatica*.

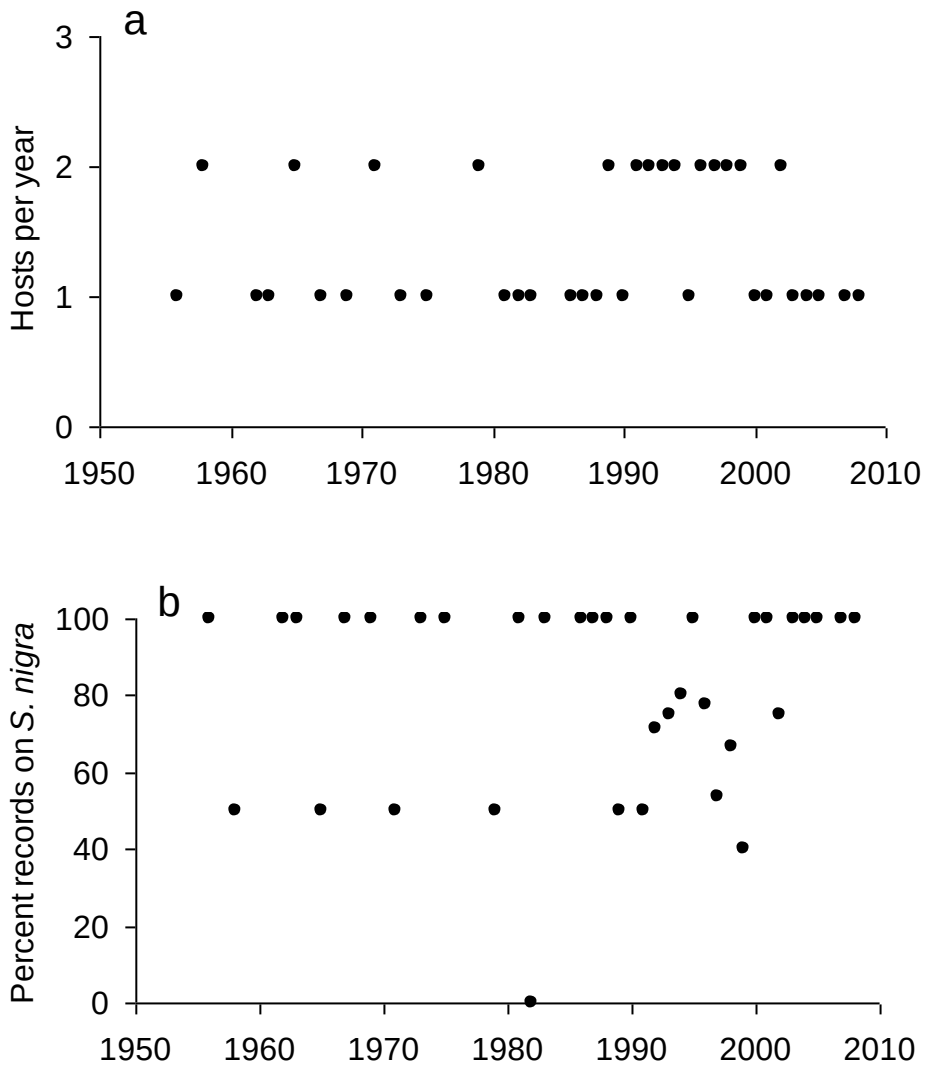


Figure 4.32 The number of hosts per year upon which *Hyphodontia sambuci* was recorded (a) and the proportion of yearly records for this species that were on *S. nigra* (b) from 1950 – 2008.

4.5.4 Discussion

Analysis of the long-term dataset has shown that: 1) *A. auricula-judae* has switched hosts over years; 2) *A. auricula-judae* has altered its fruiting period; and 2) *S. nigra* seems to host more fungal species in recent years than in the past.

There is always a concern that these changes could be due to sampling artefacts. Species accumulation curves usually show asymptotic curves or straight lines if the data are plotted on semi-log or log-log axes (Rosenzweig 2002). The shape of the curve is determined by the intensity of sampling with the number of forays per year as a function of effort. Moreover, fungal host species accumulation would be expected to follow a curve, as not every species could or would be found on any one visit. Nevertheless, it is encouraging that sampling effort was relatively constant through time. The area covered in the present study is approximately 2,828 km^2 and the number of possible localities within it is probably between 20,000 and 30,000, therefore the straight-line plot of cumulative sites obtained in the study is unsurprising. Over the period of recording, only a small fraction of the total number of possible localities has been sampled. Nevertheless, localities have been added to the total at a constant rate and thus, we might expect to see accumulation curves for individual species to either resemble that of localities, i.e. a linear relation, or to show an asymptotic curve, if the parameter measured (such as host occurrence) becomes exhausted. The accumulation curve for hosts of *A. auricula-judae* does not follow such patterns. This fungus was found only one host, *S. nigra* for 28 y and the dramatic increase in host number only started to occur after 41 y of sampling. Therefore, the apparent shift in fungal hosts is likely to mirror real biological changes rather than sampling effects. Otherwise, if this was an artefact of sampling efforts, the number of hosts would have been expected to increase at much greater rate.

Evidence in older literature suggested that *A. auricula-judae* has been fruiting occasionally on different hosts other than *S. nigra* in the UK (Gwynne-Vaughan & Barnes 1927; Ramsbottom 1944, 1953; Wakefield & Dennis 1950). Meanwhile, recent publications have also suggested a broader range of hosts (Jordan 1995; Keizer 1996; Harding 2008). It appears that *A. auricula-judae* has become much commoner on

certain hosts over the last 59 y. Furthermore, it seems to have become much more abundant on *F. sylvatica* than on other host plants. The first record on this host plant was after 29 y, since when it has become the dominant host for the fungus while there has been a corresponding decline in the records of *S. nigra.*

Analysis has shown that *A. auricula-judae* now fruits on a range of woody hosts particularly *F. sylvatica*. There is no evidence of whether this fungus has colonised wood of a wider range of species for a long time but did not fruit, or whether it was latently present within functional sapwood of a wide range of angiosperms but unable to develop overtly. The primary colonisers of twigs and branches attached to standing trees usually consist of basidiomycetes and xylarious ascomycetes that are latently present in functional sapwood (Boddy 2001; Hendry *et al.* 2002; Boddy & Heilmann-Clausen 2008). Propagules of latent invaders are considered to be extensively, but sparsely, spread within functional xylem and unable to develop until the water content is lowered. It is now evident, from isolations onto artificial culture media (Griffith & Boddy 1990), and with PCR primers specific to certain fungal taxa (Parfitt *et al.* 2010), that many species are wide-spread across angiosperm tree species but commonly only develop overt decay columns in a narrow range. For example, *Daldinia concentrica* fruits commonly on *F. excelsior* and occasionally on *F. sylvatica* in the southern Britain, and also on *Betula spp.* in Scotland, but the species can be detected in the functional sapwood of many tree species (Parfitt *et al.* 2010). In order to detect which species that actually develop as mycelia in wood depends on the abiotic conditions prevailing when sapwood begins to dry, including rate of drying and temperature (Chapela & Boddy 1988; Hendry *et al.* 2002), and both temperature and rainfall patterns have changed over the last 60 y in the UK (Jenkins *et al.* 2007). There are no reports of *A. auricula-judae* as a latent invader, but this may be simply because it was not looked for. However, if this species arrives as a later coloniser, rather than being a latently present primary coloniser, changes to the abiotic environment could have influenced which host it establishes upon. Combative interactions are commonly the main driver of fungal community development. The outcomes of such interactions, i.e. whether a fungus replaces, is replaced by, or deadlocks with an opponent, can be greatly

influenced by the abiotic environment, including temperature, water potential, gaseous regime and resource size (Boddy 2000; Toljander *et al.* 2006; Woodward & Boddy 2008). Therefore, changes in the UK climate since the 1970s, reported by Fitter & Fitter (2002), may have resulted in host shifts in the balance of fungal competition within dead beech, elder and other wood species. Apart from fungi, host shift affects due to climate change have also been seen in other organisms, for example the mountain pine beetle (*Dendroctonus ponderosae)* which is a native insect of the pine forests of western North America. Factors such as reduced minimum winter temperature, increased summer temperatures and reduced summer precipitation during recent decades have caused the populations to periodically erupt into large-scale outbreaks (Kurz *et al.* 2008). In addition, community shifts issue of regime in ecosystems has occurred at the alpine zones of Northwest Yunnan where the herbaceous ecosystem has shifted to a shrub-dominated ecosystem due to increasing temperatures since 1970s (Brandt *et al*. 2013). With shrub expansion rates approaching 70% in some areas, this may lead to the contraction of meadow areas followed by the reduction in endemic plant biodiversity locally (Rejmanek & Rosen 1992) and regionally (Eldridge *et al.* 2011; Ratajczak *et al.* 2012; Brandt *et al.* 2013).

In addition to changes in host range, the timing of fruiting of *A. auricula-judae* has also altered with an earlier fruit body appearance, perhaps reflecting mycelial activity at different times of year and/or difference in the triggering of fruiting. In this respect, it is similar to many other fungal species that have shown advanced autumnal fruiting patterns (Gange *et al.* 2007). Moreover, coincidental with the change in fruiting pattern is the fact that other species have begun to fruit on *S. nigra*, the main host of *A. auricula-judae*. These changes are coincidental with the altered patterns of rainfall and increased warming of the climate in Southern England since 1975 (Fitter & Fitter 2002). A significant relation between the appearance of fungal species and the preceding average temperature for the month of March was found with earlier fruiting in years when the March temperature was higher (Kauserud *et al.* 2009). Spring temperatures in Southern England have increased over this time and this has been shown to influence the fruiting of vernal fungi (Mattock *et al.* 2007; Kauserud *et al.*

2010). Appearance of fungal fruit bodies has usually been correlated with prevailing temperatures and rainfall close to the start of the fruiting season (Straatsma *et al.* 2001; Krivstov *et al.* 2003), but recent data show that fungal fruiting can respond to climatic variables over longer time scales than was previously thought. Indeed, Kauserud *et al.* (2010) have shown that fruiting of vernal fungi is influenced by prevailing temperatures in the previous summer.

This study may not explain the real cause and effect of the fungal fruiting pattern, let alone be certain that climate change has been the main driver of the host range changes and fruiting times of *A. auricula-judae.* Without doubt, there have been significant changes in atmospheric pollutants, levels of nitrogen deposition and soil chemistry in the UK over the last 20 y, and these have been coupled with changes in plant and animal communities (Matejko *et al.* 2009; Morecroft *et al.* 2009). Such changes could impact upon the population dynamics and physiology of plants such as *S. nigra,* which in turn may lead to alterations in the host preference of a fungus such as *A. auricula-judae*. *S. nigra* is commonly but not exclusively associated with hedgerow habitats (Atkinson & Atkinson 2002). According to Barr & Gillespie (2000), the amounts of hedgerows have declined by 23% between 1984 and 1990 nationally. Thus, although *S. nigra* is an extremely common shrub and resistant to most environmental changes such as pollutants (Atkinson & Atkinson 2002), it is plausible that climate change factors other than temperature, or those unrelated to climate change, have contributed to the changes in the biology of *A. auricula-judae* reported here. Therefore, it would be beneficial to investigate whether factors such as atmospheric pollutants, gaseous regime or changes in soil chemistry have potential to influence the alteration of growth and fruiting of saprotrophic fungi. Such studies could be conducted by combining experimental studies with data gathered from databases such as that analysed here.

An understanding of fungal-host associations and macrofungal diversity are as critical to the conservation of rare fungi as the management of habitats (Lonsdale *et al.* 2008). In fact, even a simple data set such as that used in this study has shown that there has been a constant change in both fungal-host associations and macrofungal diversity

which must be taken into consideration when formulating conservation strategies. If fungi are changing their hosts over time, this could have important consequences for their conservation. In the majority of cases, our notion of fungal rarity is based on fruit body appearance, which is known to be an inaccurate measure of fungal presence (Dahlberg *et al.* 1997). Meanwhile, molecular methods offer great promise for rare species detection (e.g. Parfitt *et al.* 2005) and of latently present fungi (Parfitt *et al.* 2010), however, these too are subject to sampling errors (Avis *et al.* 2010). There is little substitute for long-term recording, as short-term studies often show little change in fungal population dynamics or community structure (Berglund *et al.* 2005). Nevertheless, such long-term data sets are rare, though inspection of herbarium specimens may be useful to obtain valuable information. These data sets have so far been used for studies on phenological changes (Gange *et al.* 2007; Kauserud *et al.* 2008,2010,2012) and could also be used for host range studies such as that reported here and also to find out other environmental factors that could potentially triggers the change in fungal fruiting patterns particularly in the UK.

The data suggest that changes in host range or abundance of certain fungal species could be occurring in response to climate change. Some species may alter their host range, some may broaden their geographical range and become commoner, while others may see retractions in their range and become rarer. These changes may appear due to the altered competitive abilities, or possibly lack of resource availabilities, which influenced by changing temperatures (Toljander *et al.* 2006).

Chapter 5

Climate effects on fungal fruiting patterns in the UK

5.1 Introduction

Studies examining the influence of environmental factors on fruit body production have been conducted since the 1930s (Vogt *et al.* 1992; Straatsma *et al.* 2001). Rainfall and temperature are two factors that are often discussed (e.g. Abell *et al.* 2006; de Aragon *et al.* 2007; Krebs *et al.* 2008; Pinna *et al.* 2010), but to what extent these factors affect the fruiting phenology is still unclear. There are also studies that involve modelling with rainfall and temperature as explanatory variables (Eveling *et al.* 1990; Johnson 1994; Straatsma *et al.* 2001; Salerni *et al.* 2002; de Aragon *et al.* 2007; Newbound *et al.* 2010). These analyses typically investigate the influence of climate by considering how well discrete periods of rainfall or temperature explain variation in phenology (Newbound *et al.* 2010). There are growing numbers of studies showing that phenology is an indicator of global climate change (Visser & Both 2005; Menzel *et al.* 2006; Yang & Rudolph 2010), however the effect of climatic factors on fungal fruiting phenology particularly rainfall and temperature, have yet to be discussed in detail.

Besides rainfall and temperature, several other factors that are important for triggering primordia formation and the production of fruiting bodies also have been identified, such as a need for high substrate moisture (e.g. soil), sudden drops in temperature to initiate primordia, effect of evapotranspiration and light and dark periods of specific length for both initiation and development of mature fruiting bodies (de Aragon *et al*. 2007; Newbound *et al.* 2010). Furthermore, nitrogen deposition from the atmosphere is also found to have an influence on the formation of above-ground fruit bodies (Lilleskov 2001; Gillet *et al.* 2010; Tarvainen *et al.* 2012).

Since fruit bodies are comparatively easy to quantify, their occurrence has become an important parameter in the investigation of effects of environmental change on the

macrofungal flora (Wallenda & Kottke 1998). To achieve this, elaborate and long-term data-sets are required to draw any conclusions on the occurrence and the behaviour of fruit bodies and also to monitor any fruiting trends across time. A number of long-term studies have now been published on fungal phenology (Gange *et al.* 2007; Mattock et al. 2007; Kauserud *et al.* 2008; Moore *et al.* 2008; Kauserud *et al.* 2010; Newbound *et al.* 2010; Kauserud *et al.* 2012), species richness and abundance (O'Dell & Ammirati 1999; Straatsma *et al.* 2001; Smith *et al.* 2002) and fungal-host associations (Saikkonen *et al.* 1998; Gilbert *et al.* 2008; Gange *et al.* 2011). Together, this have given the impression that climate plays major role in fruit body production.

The present study describes the relationship between climatic parameters (e.g. temperature and rainfall) and fungal fruiting patterns over 58 y of recording and the extent these parameters affect the fruiting pattern of functional groups and within genera. Besides that, the effect of temperature on fruiting patterns of species with different nutritional modes e.g. mycorrhizal and saprotrophic fungi, also will be investigated. Previously, in Chapter 3, it was found that mycorrhizal and saprotrophic species showed different behaviour. Most saprotrophic species reacted with earlier appearance, while most mycorrhizal species tend to have later appearance. In addition, these groups also show differences in their last fruiting date; saprotrophs showed earlier LFD compared to mycorrhizal species whereas most mycorrhizal species tend to have later average fruiting dates than saprotrophic species. Therefore, any effect of temperature on fruiting aspects for each trophic group in this study could explain the true relation between fruiting phenology and temperature.

The overall goal of this study was to identify if and which climatic factors show most influence on the observed variation in the phenology of macrofungal communities in the previous study in Chapter 3. Moreover, I also tested the following hypotheses: i) the relationship between phenology of each functional group and temperature parameters varies from year to year and ii) there are differences in climate-induced responses between mycorrhizal and saprotrophic species in the dataset. Furthermore, the results of the responses of genera in this study will be compared with phenology

results of the same genera tested in Chapter 3 to test whether changes in the phenology of species is related to the changes in temperature over years.

5.2 Methodology

5.2.1 Fungal phenology data

The fungal data used for the study are those previously used in Chapter 3 and 4 of the thesis. In this chapter, all ten functional groups; grass, mycorrhizal coniferous, leaf litter, mycorrhizal deciduous, live leaves, needle litter, manure, soil, living trees and dead wood described in Chapter 3 were used. Besides that, seven genera that were previously analysed in the fungal phenology study i.e. *Amanita, Clitocybe, Collybia, Inocybe, Lactarius, Mycena* and *Russula* also were studied. Responses of each taxonomic unit (species, genus, functional group) towards different climate parameters also were investigated.

5.2.2 Weather data

The weather data were collected from Southampton Weather Station which is located 30 km from New Forest, where all fungal species were recorded. A total of six parameters were selected for this investigation i.e. mean annual maximum air temperature (the average day temperature recorded per annum), mean annual minimum air temperature (the average night temperature recorded per annum) cumulative temperatures, minimum and maximum (the sum of daily temperatures over year, for night and day, respectively (all temperatures are in °C), mean annual rainfall (mm) and mean relative humidity (%). Regarding cumulative air temperature, this was calculated as the accumulated temperature (maximum or minimum) on a daily basis each year and up to the date when FFD or LFD occurred per taxonomic group (i.e. functional group). These cumulative temperatures per year were then regressed against the respective FFD and LFD.

These parameters were checked for differences among years, and monthly, yearly and decadal patterns and trends over time were examined with Analysis of Variance and

linear regression. Also, the phenological variables for each of the fungal functional groups (i.e. first fruiting date (FFD), last fruiting date (LFD) and length of fruiting season (RANGE), were regressed against all climatic parameters examined in this study to identify correlation between the two variables.

5.2.3 Statistical analysis

At first, analysis of variance (ANOVA) was performed to check for significant differences of fruiting phenological variables (mean FFD, LFD and range per functional group) against averaged meteorological data. Moreover, analysis of covariance (ANCOVA) was performed to test for differences among fruiting phenological data (dependant variables) against different taxonomic groups, viz. functional group, genus or species (categorical variable) and meteorological parameters (continuous variable). Trends over time with climatic variables were also investigated by performing linear regression analysis between fruiting phenological characters (i.e. FFD, LFD, range) (dependant variables) per taxonomic unit (i.e. functional group) against meteorological parameters (independent variable). All data analyses were conducted at the yearly and decadal scale (mean value of each meteorological parameter per decade). To describe the relationship between FFD and LFD with the respective cumulative temperatures, the distance-weighted least squares fit was used.

Apart from direct statistical relationship, interaction (factorial ANCOVA and regression) and lag effects (auto- and cross- correlation) among all variables were also examined. Thus, the combined effect of meteorological factors (interaction; independent variables) or the delayed effect of meteorological factors (cross-correlation at various scales, monthly to decadal; independent variable) on fungal fruiting phenology (dependant variable) were examined. Regarding the latter potential effect, it is already widely known for other long-living organisms that sometimes quite strong auto-correlation patterns exist in their growth habits in both plants (e.g. Pfister & Stevens 2002) and animals (e.g. Peakall *et al.* 2003). Therefore, it was considered a key element to check for the ability of fungi to `remember' environmental changes affecting their

fruiting phenology. If such a `memory' indeed exists, it would probably be a useful tool for understanding (or even predicting to a certain extent) fungal ecology. To achieve the above, all relative analyses were performed in a yearly basis checking up to 10 year-lags and, when statistical significance was detected up to that period, data were tested in a decadal scale, checking for about up to half of the total period (25-year lags).

In all the above analyses, significance level *p*, coefficients of determination R^2 and regression coefficients were estimated. The remaining noise and goodness-of-fit were checked by examining the residual distribution.

5.3 Results

5.3.1 Temporal patterns of meteorological time-series

Over the years, the average decadal minimum temperature in the New Forest study sites has increased from 6.7°C in 1950s to 8.8°C in the 2000s, with an average increase of 0.4°c for every decade. Temperature rise was not apparent in the 1950s, but become so in the 1970s, in which the increase of the average temperature per year was between 0.1°C and 0.2°C. However, the average annual minimum temperature also began to rise dramatically after the 1980s with an increase of 0.6°C in the 1990s, and 10 years later, the temperature had increased by 1°C in the year of 2000 (Figure 5.1).

On the contrary, the average decadal maximum temperature over the course of study period did not show a similar trend to minimum temperature. The average decadal maximum temperature fell by 0.5°C within the first thirty years since 1950s but has slowly increased since the 1980s. There was a substantial temperature rise between the 1980s and 1990s, where an increase of 0.7°C was recorded. The average decadal maximum temperature has been steady with an average increase of only 0.2°C in the last 10 years (Figure 5.1). Meanwhile, average yearly rainfall in the study sites showed

fluctuations since the beginning of 1950s until early 2000s. Year 1960 had recorded the highest average annual rainfall, indicating this year was the wettest year compared to the other time during study period while 1974 was the driest year (Figure 5.2).

Meanwhile, relative humidity (RH) data were only obtained from 1992-2007, but also displayed fluctuations across years (Figure 5.3). The highest percentage of RH was recorded in 2000 while the lowest RH record was in 1995. The average of RH ranges from 79% to 85% across 15 y.

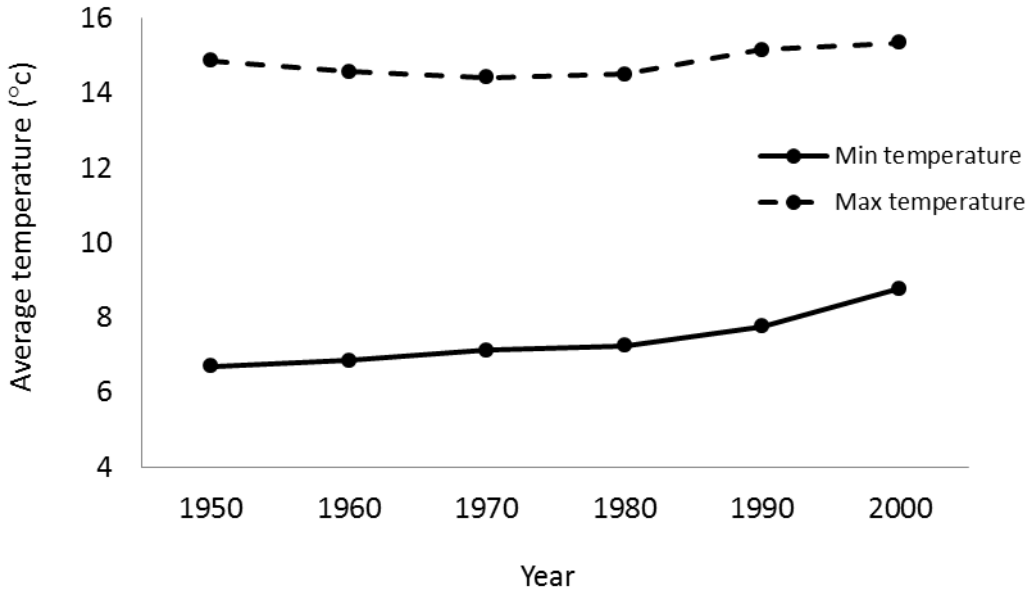


Figure 5.1. Long-term trends of average decadal a) minimum temperature and b) maximum temperature (°c) in the study sites over the period 1950-2008.

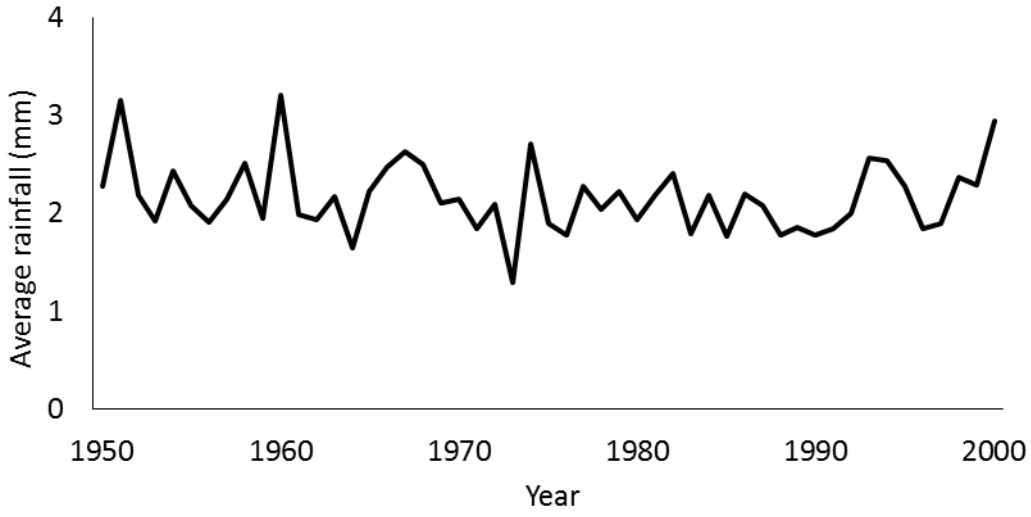


Figure 5.2. Long-term average yearly rainfall amount (mm) over the period 1950 -2001.

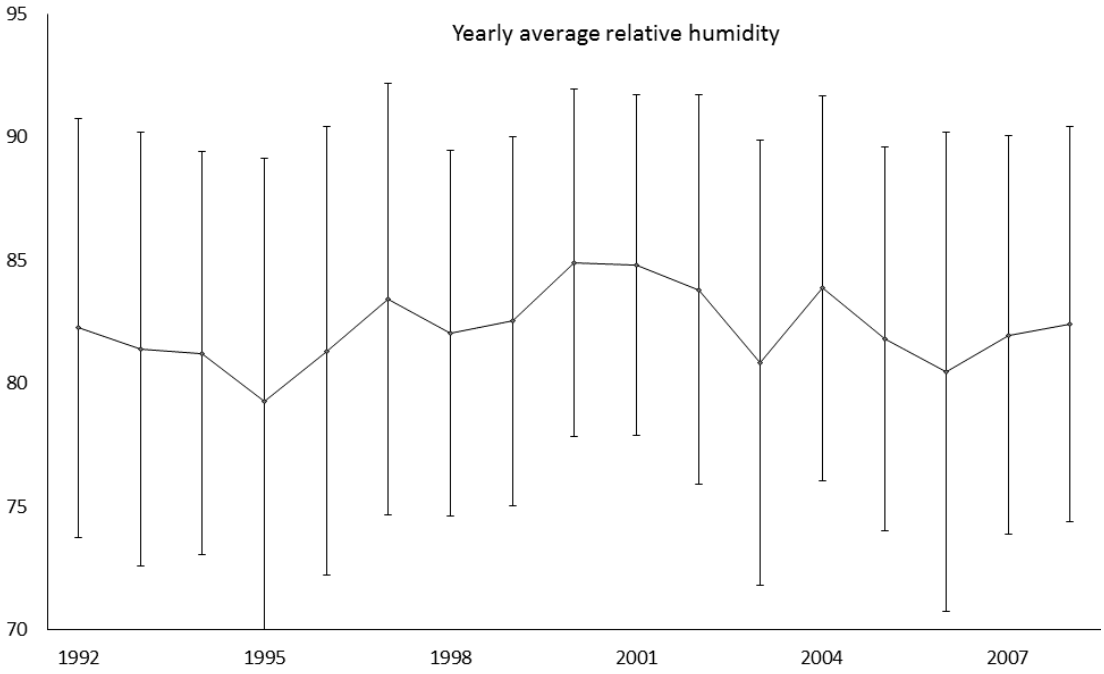


Figure 5.3 The annual average of relative humidity from 1992 to 2008.

5.3.2 Relationship between weather data and fungal fruiting patterns

a) Direct comparisons of fungal fruiting data against yearly temperatures

Originally, there were 368 fungal species recorded in the data set comprising both spring and autumnal species. However, only autumnal species (n = 353) were considered for this analysis to avoid bias in fruiting season and potentially opposing responses depending on the taxon examined. Of the four meteorological parameters analysed, only minimum and maximum temperature showed significant relations with almost all fruiting aspects. ($p \leq 0.05$). There was no significant trend in the rainfall time-series and relative humidity ($p \geq 0.05$). The minimum and maximum temperatures were found to show different responses at different temporal scales. The maximum temperature only showed increasing trend when regressed against LFD and Range at the annual scale.

b) The relations of fungal fruiting data with cumulative temperature

Stronger relationships were displayed when FFD, LFD and range was regressed against cumulative average decadal minimum temperature. The FFD of most autumnal species has become earlier, as minimum temperature rose and similar trends were also detected in cumulative temperature and in the preceding average decade temperature. Furthermore, a positive relation was also found with range of season, where expansion of fruiting season was detected for autumnal species over decades when cumulative minimum temperature rises. On the contrary, LFD displayed weaker trends in relations to cumulative decadal minimum temperature over time.

Most functional groups showed strong relationships between their phenological variables i.e. FFD and LFD, and the cumulative maximum and minimum temperatures throughout the study period ($p<0.001$ in all cases) (Table 5.1). However, the strength of the relationship (R^2) between FFD and LFD with both temperature aspects was different from one functional group to another, indicating that each group interacts in a different way to different temperature aspects. Moreover, of the two phenological

variables analysed, FFD has shown stronger trends with temperature than LFD. In terms of fruit body appearance, dead wood fungi and manure fungi displayed strong trends with minimum temperature. On the other hand, FFD of dead wood and grass fungi showed greater association with maximum temperature (Table 5.1). Fungi found on live leaves group were excluded from this analysis, because the fungi on live leaves in this data set mainly grow during spring.

Almost every functional group's FFD appear to be associated with daily heat sums ($p<0.01$, $R^2>0.6$) (Figure 5.4). Furthermore, all functional groups also showed increasing trends, indicating that across years, daily heat sums are getting higher and the appearance of these autumnal fungal species tend to be delayed. The appearance of wood decay fungi and fungi found on manure displayed the most significant relation with daily heat sums compared to the other functional groups ($R^2=0.83$).

Meanwhile, LFD for most functional group also showed significant relations with daily heat sums from 1950 to 2000 ($p<0.01$, $R^2>0.6$) but weaker responses than their FFD (Figure 5.5). The LFDs of mycorrhizal fungi found under coniferous trees showed the weakest relationship with daily heat sums ($R^2 = 0.4$) compared to the other functional groups.

Table 5.1: (One-way) Linear regression results of phenological variables of 353 autumnal fungal species against cumulative annual minimum and maximum air temperature for 10 functional groups. Significance level p, and coefficients of determination R^2 are given.

Functional group	**Phenological variable**	**Cumulative temperature**			
		Minimum		**Maximum**	
		p	***R²***	***p***	***R²***
Dead wood	FFD	<0.001	0.83	<0.001	0.95
	LFD	<0.001	0.61	<0.001	0.85
Grass	FFD	<0.001	0.80	<0.001	0.95
	LFD	<0.001	0.72	<0.001	0.90
Leaf litter	FFD	<0.001	0.75	<0.001	0.91
	LFD	<0.001	0.63	<0.001	0.84
Living trees	FFD	<0.001	0.77	<0.001	0.92
	LFD	<0.001	0.62	<0.001	0.85
Manure	FFD	<0.001	0.83	<0.001	0.94
	LFD	<0.001	0.71	<0.001	0.90
Myc. conifer.	FFD	<0.001	0.60	<0.001	0.88
	LFD	<0.001	0.44	<0.001	0.80

Myc. decid.	FFD	<0.001	0.74	<0.001	0.91
	LFD	<0.001	0.67	<0.001	0.86
Needle litter	FFD	<0.001	0.67	<0.001	0.89
	LFD	<0.001	0.58	<0.001	0.83
Soil	FFD	<0.001	0.75	<0.001	0.91
	LFD	<0.001	0.66	<0.001	0.84
Total	**FFD**	**<0.001**	**0.78**	**<0.001**	**0.93**
	LFD	**<0.001**	**0.64**	**<0.001**	**0.86**

Table 5.2. (One-way) Linear regression results of phenological variables against time for 7 genera. Coefficients of determination R^2 and (in parenthesis) regression slopes are given. '***' Sign indicates p<0.001, '**' 0.001<p<0.01 and '*' 0.01<p<0.05 and 'ns' denotes a non-significant relationship. '+' Sign means a parallel change, whereas '-' an inverse change.

Genus	**Phenological variables**		
	FFD	**LFD**	**Range**
Amanita	***	ns	***
	0.26 (-0.58)		0.27 (+0.57)
Clitocybe	*	***	***
	0.07 (-0.42)	0.32 (+0.77)	0.55 (+1.24)
Collybia	***	ns	***
	0.38 (-1.00)		0.48 (+1.28)
Inocybe	***	***	***
	0.32 (+0.96)	0.65 (+1.73)	0.27 (+0.77)
Lactarius	Ns	***	***
		0.30 (+0.43)	0.25 (+0.49)
Mycena	***	***	***
	0.21 (-0.55)	0.21 (+0.52)	0.46 (+1.07)
Russula	Ns	***	***
		0.38 (+0.68)	0.47 (+0.71)

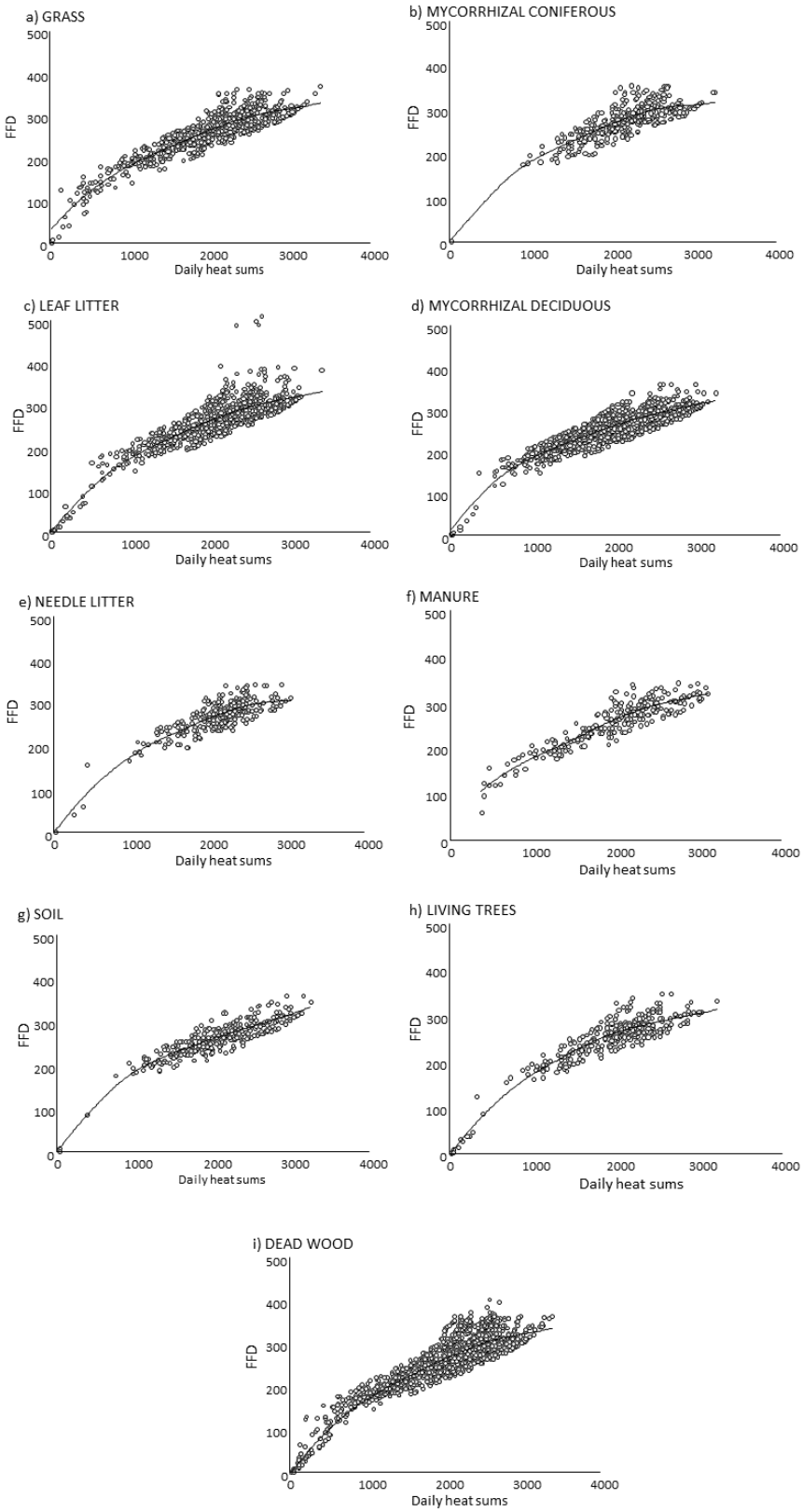


Figure 5.4. Responses of first fruiting dates against daily heat sums from 1950-2000 for each functional groups. a) grass, b) mycorrhizal coniferous, c) leaf litter, d) mycorrhizal deciduous, e) needle litter, f) manure, g) soil, h) living trees, i) dead wood. Lines were plotted using a distance weighted least squares method.

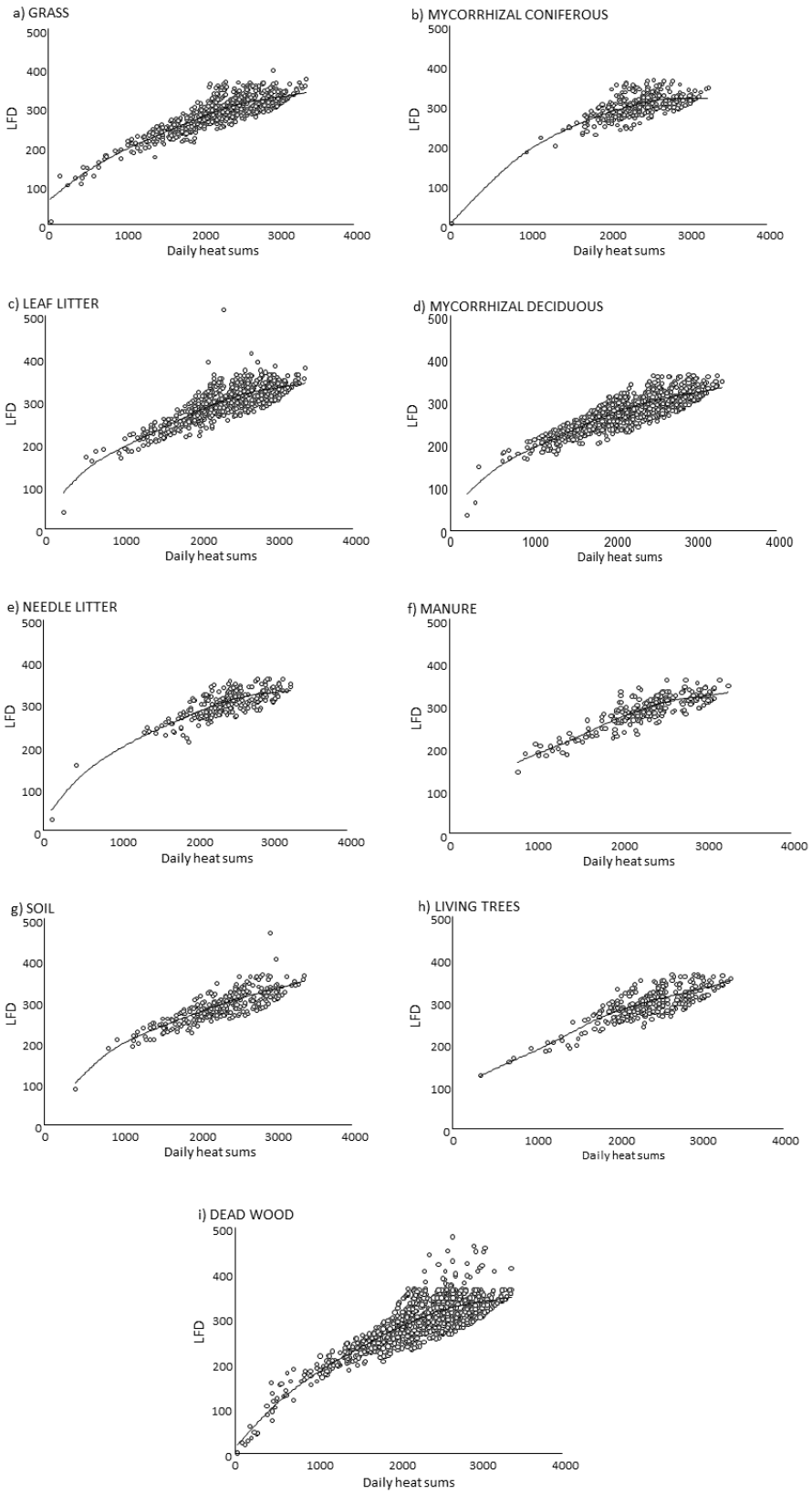


Figure 5.5. Responses of last fruiting dates against daily heat sums from 1950-2000 for each functional groups. a) grass, b) mycorrhizal coniferous, c) leaf litter, d) mycorrhizal deciduous, e) needle litter, f) manure, g) soil, h) living trees, i) dead wood. Lines were plotted using a distance weighted least squares method.

e) Lag-effect of fungal fruiting phenology with temperature

Another significantly statistical relationship found between mainly minimum temperature and fungal fruiting phonological characters was a delayed effect of the second upon the first. This lag effect was observed in most functional groups, thus providing evidence on fungal fruiting data serial correlation and also cross-correlation with temperature indices. In terms of FFD, the minimum temperature in prevailing years seem to influence the later appearance of all functional groups with the maximum lag-effect have taken as early as 12 y (e.g. mycorrhizal deciduous). Of the ten functional groups examined, nine i.e. fungi found on dead wood, grass, leaf litter, live leaves, living trees, mycorrhizal coniferous, mycorrhizal deciduous, needle litters and soil have displayed a persistent `memory' which affect present FFD based on up to past 12 y temperature (Table 5.2).

On the other hand, eight functional groups (excluding fungal found on live leaves and mycorrhizal fungi under coniferous trees) showed significant relations with minimum temperature, with LFD being influenced by minimum temperature with a lag effect up of up to 12 y. This suggests that the records of minimum temperature obtained during the previous 12 y period are significantly affecting the present LFD occurence. Meanwhile, mycorrhizal fungi found under coniferous trees showed no trend of lag-effect in relation to minimum temperature across the fruiting time series.

Table 5.3: Cross- correlations of fruiting season variables of 10 functional groups of fungi with lagged minimum temperature time-series. Numbers of lags (in years) and (in parenthesis) correlation coefficients are given.
'+' sign indicates a positive change, whereas '-' an inverse change; 'ns' denotes a non-significant relationship.

Functional group	Variable	Minimum temperature
Dead wood	FFD	**0-3 -(0.35-0.74)**
	LFD	**8 +(0.28)**
	Range	**0-5 +(0.30-0.73)**

Grass	FFD	**0-3 -(0.31-0.41)**
	LFD	**0-2, 4, 7-9 +(0.28-0.44)**
	Range	**0-10 +(0.31-0.69)**
Leaf litter	FFD	**0-2 -(0.40-0.53)**
	LFD	**0-8 +(0.31-0.57)**
	Range	**0-7 +(0.29-0.74)**
Live leaves	FFD	**0-9 -(0.36-0.67)**
	LFD	**0-3, 6 -(0.31-0.58)**
	Range	**0-5, 7-9, 11 +(0.33-0.44)**
Living trees	FFD	**0-2 -(0.28-0.45)**
	LFD	**0-5, 7, 8, 10 +(0.29-0.51)**
	Range	**0-10 +(0.32-0.75)**
Manure	FFD	**0, 1 -(0.30-0.34)**
	LFD	**3-5 +(0.29-0.33)**
	Range	**0-10 +(0.29-0.47)**
Mycorrhizal coniferous	FFD	**0-4 -(0.36-0.55)**
	LFD	**ns**
	Range	**0-4 +(0.29-0.46)**
Mycorrhizal deciduous	FFD	**12 +(0.31)**
	LFD	**0-10, 12 +(0.33-0.67)**
	Range	**0-7 +(0.30-0.68)**
Needle litter	FFD	**0-4 -(0.29-0.54)**
	LFD	**0, 2, 3, 11 +(0.30-0.33)**
	Range	**0-7, 9 +(0.30-0.67)**
Soil	FFD	**1-4, 6-8 +(0.27-0.38)**
	LFD	**0-9 +(0.31-0.64)**
	Range	**0-2 +(0.28-0.55)**

5.4 Discussion

The present study demonstrated that air temperature substantially affects the timing of first fruiting dates (FFD) and last fruiting dates (LFD). FFD shows stronger trends of relationship with temperature, while LFD is much weaker. Thus, as temperature increases, autumnal species tend to fruit earlier. Temperature seems to influence in a similar way also plant phenology, as numerous experimental studies have documented (Larcher 1995; Price & Waser 1998; Menzel & Fabian 1999; Fitter & Fitter 2002). Moreover, by considering the effect of cumulative temperature on FFD and LFD occurrence and hence for all functional groups, it is evident that air temperature, to a certain degree, is the driving factor for the earlier shift of the autumnal fungal fruiting season. Finally, as this interaction appears to be a very persistent one, displaying delayed effect of up to three decades, it is remarkable how high the relevant responsive ability of fungi is. According to IPCC (2001), temperature as well as phenology has changed most noticeably after the mid-1970s; the fact that increasing temperature has influenced phenological patterns of fungal fruiting over time and, hence in an additive way, solidifies previous findings suggesting that fungal species that were formerly reported only to fruit in autumn, now also fruit in spring (Gange *et al.* 2007; Moore *et al.* 2008).

On the other hand, rainfall and relative humidity displayed no significant long-term trends during the study period and, thus, did not play a significant role on fungal fruiting timing in the long-term. Absence of trends may as well be justified by the great variance observed in these time-series. Previous research on the interaction of fungal fruiting with rainfall was also conducted by Gange *et al.* (2007) and an inverse relationship was found. This distinction from the present study, and although the same dataset was used for both studies with additional records in this study for only the period 2005-2008, is probably related to the timescale examined. As Gange *et al.* (2007) processed monthly values of rainfall (and temperature), relationship with fungal fruiting timing was more prominent. It seems that specific climatic factors (among which rainfall) affect phenological characters like fruiting of macrofungi at finer

timescales. Evidence on this provides the very strong relationship between daily cumulative temperatures and fungal fruiting start and end dates, which were investigated for in this study. Therefore, depending on the relationship to be examined and the factor analysed, different timescales should be tested each time.

Fruiting phenology of all functional groups in this study also have been shown to be related to the daily heat sums (accumulated thermal time). Across 58 y, daily heat sums per year are getting higher and causing earlier shifts to both FFD and LFD of autumnal species. However, the effect of daily heat sums towards FFD and LFD is different as FFD displayed stronger relation to the temperature compared to LFD. As the observed changes were more directed to FFD than LFD, it is likely that air temperature has greater effect on the early stage of autumnal fruit body formation than the disappearance of these fungi. However, the fact that temperature showed weaker trend in LFD, this demonstrates that temperature alone cannot explain all these shifts. Kauserud *et al.* (2012) asserted that later fruiters are continuing to fruit due to higher temperatures during autumn fruiting season, however, in this study several other environmental factors have not been taken into account. Therefore, according to Gange *et al.* (2013), in their response letter to Kauserud *et al.* (2012), also emphasised on the importance of resource availability, which also plays a role in determining the disappearance of saprotrophic fruit bodies. Besides climate effects, nutrient resources also needed for basidiocarp production, therefore, resource depletion in the mycelium could also affect species LFD. This is also confirmed by related experimental results by Damialis (pers. commun.) who has experimentally tested fungal responses under increasing temperatures and in variable nutrient availability: it has been found that most species produced more spores in richer nutrient media and higher temperatures and particularly regarding nutrient levels, when they are in abundance LFD seems to be delayed. This is totally plausible under the current environmental change, as nutrient deposition and eutrophication of the planet are expected to linger the end of fungal fruiting season. Apart from that, many other factors, such as habitat change, atmospheric deposition, and recorder behaviour can also be considered for the changes observed.

Furthermore, the finding that those species with different nutritional modes, such as saprotrophic and mycorrhizal fungi, are likely to be affected differently by minimum temperature (night temperature) highlighted how different species may be particularly vulnerable to increases in both maximum (day) and maximum (night) time temperatures. Cheesman & Winter (2013) indicated that productivity of plants is often limited by seasonal minima in temperate areas, and suggested that an increase in temperature could be related to the extension of the plant's growing season or a shift towards a temperature optimum for growth. This may also applicable to the fungal community structure, as both fungi and plants often rely on each other in the forest ecosystems. According to Davis (1984), the community effects arise because species vary in their responses to climate including both the magnitude and the timing of responses (phenology). Some animals including hummingbirds, Belding's ground squirrels and butterflies are able to track climate closely, reacting to conditions each year (Gass & Lertzmen 1980), while others such as plants respond so slowly, that only long-term climatic trend have any observable impact on them (e.g. Iversen 1944; Menzel *et al.* 2001; Fitter & Fitter 2002). In addition, variation in responses of fungi to temperature have also been shown by Damialis *et al.* (unpublished) who discovered different rates of competition capacity are displayed by endophytic fungal species, proving that some species tend to be highly competitive regardless of the environmental regimes (e.g. *Alternaria alternata*), whereas others displayed varying behaviour depending on temperature and nutrient availability (e.g. *Botrytis cinerea*). In terms of the effects of climate on fruiting phenology of fungi of different nutritional mode, the two groups displayed almost a similar pattern in their first FFD, LFD and length of fruiting season. However, the causative mechanism in these two groups may be different due to separate functional contexts (Lindahl *et al.* 2001). Kauserud *et al.* (2012) suggested that saprotrophs may be directly affected by the abiotic environment, while mycorrhizal fungi will also be affected indirectly, via effects on the host plants.

The effects of various climatic factors on fungal fruiting phenology, and especially those of temperature, seem to be more profound than originally thought. Occurrence

of lagged responses in fungi (i.e. fruit body occurrence in relation to temperature the year before) indicated that the rise in preceding average decade temperature encourage the earlier appearance of autumnal species. The result of this study has been also implied by Kauserud *et al.* (2012) who noted that temperature in later preceding year has greater effect on fungal fruiting patterns and the fact that the state of below-ground mycelia of fungi, including the ability of primordia to fruit is determined by climatic conditions over more than a single year was evidently true. Of course this also statistically expected, due to the strong autocorrelation observed in long-term natural ecosystems; it is well known that environmental data collected over consecutive time periods are often serially correlated, with data closely associated having higher correlations between them than data farther apart, which is particularly true for long-living organisms (Chatfield 1989). However, in the present study more comprehensive analysis managed to demonstrate the projected amount of years for specific groups and also extended up to genus level compared to previous relevant studies. Besides that, the lag-effect knowledge on the effect of climate towards fruiting phenology could also offer a new spectrum in fungal community studies as this will enable us to predict the fruiting phenology of autumnal species: with such high responsive ability of fungi and with such persistent 'memory' related to past temperature records, it is expected in terms of community structure, but also distribution, abundance and phenology, that fungal behaviour will be potentially predicted to a certain extent, which, from a conservation perspective, is really important under the ongoing climate change, so as to define the optimum upper and lower limits of fungal growth and distribution range and thus protect sensitive species in the future.

Overall, this study displays important implications for researchers to examine phenological change in fungal community and the extent to which climatic factors triggers the changes of fruiting phenology. Although this study managed to identify which climatic factors showed significant correlation with changes in fruiting phenology, however, we are still lacking of the knowledge on to which external factors affect the fruiting the most. Therefore, extensive studies that combine as many

environmental factors as possible and that investigate for the interaction effect and at various timescales would be recommended to answer the question.

Chapter 6

Do *Hypholoma fasciculare* individuals fruit more than once a year?

6.1 Introduction

Saprotrophic fungi are the primary decomposing agents in temperate woodland ecosystems (Hättenschwiler *et al*. 2005; Baldrian & Valášková 2008). Their filamentous mycelial networks grow throughout the soil-litter interface, forming systems which contribute significantly to the total ecosystem biomass and respiration (Post *et al.* 1982; Bardgett 2005; Crowther *et al.* 2011). During mycelial extension, competitive interactions take place at a distance, via antagonistic volatile organic compound production, or following mycelial contact, and commonly result in the replacement of one fungus by another (Boddy 2000; Crowther *et al.* 2011). The outcomes of these mycelial interactions determine fungal dominance and community composition in litter resources and soil (Boddy 2000; Crowther *et al.* 2011). Saprotrophic fungal community composition, determined by the outcome of competitive mycelial interactions, is one of the many key factors affecting soil nutrient mineralisation and decomposition rates.

Many studies have been carried out regarding reactions between different fungal species that grow together on the same host and the effects of these responses on the hosts (e.g. Pereira *et al.* 2012). These studies can either be observed with culture techniques (e.g. Shaw *et al.* 1995; Baar & Stanton 2000; Werner *et al.* 2002; Mucha *et al.* 2006; Sharma *et al.* 2010; Pereira *et al.* 2012) or on natural substrates using a microcosm system (e.g. Lindahl *et al.* 1999; 2001; Leake *et al.* 2001) and tell us that one species does compete with another to keep on surviving. Responses of interactions are varied, depending on the individual species and their combination, nutrient availability, and amount and quality of the carbon substrates on which the fungi grow (Lindahl *et al.* 1999; 2001; Koide & Kabir 2001; Werner & Zadworny 2003; Pereira *et al.* 2012). Meanwhile, other fungal interactions with other organisms also have been studied, e.g. interactions between fungi and soil organisms (e.g. Fitter &

Garbaye 1994), plants (e.g. Borowicz & Fitter 1990; Gange & West 1994), bacteria (e.g. Vaidya *et al.* 2005) and insects (e.g. Gange & Bower 1997).

Previous studies have focused on competitive interactions between fungal species and other organisms, without paying much attention to the intra-specific interactions that may occur within one individual of a species. A recent study by Gange et al. (2007) has found that several autumnal species tend to be also found fruiting in spring since the 1970s. They have suggested that mycelium of certain species must be active in late winter and early spring as well as late summer and autumn, suggesting increases in decay rates in forests. Similar findings were also found by Kauserud *et al.* (2010) suggesting that climatic conditions have influenced below-ground mycelia over a longer time period before fruiting which has led to multiple fruiting of fungi.

To my knowledge, there is still no study conducted to determine whether the same individuals are producing fruit bodies multiple times throughout the year or the following years. This is an important fact to determine. If the same individual is now fruiting several times a year, this implies greater mycelial growth, use of resources and decomposition rates in forests. However, if different individuals fruit at different time, this offers the potential for significant divergence within the species, leading to the ultimate possibility of evolutionary change. Therefore, an inoculation method was used to observe any interactions of *H. fasciculare* in three different sites in Southern England. *H. fasciculare* is one of the widely distributed wood-decay fungus that commonly appears in dense clusters on decaying wood and is abundant in the autumn (Arora 1986). Besides that, this species also grows in large clumps on dead wood and decaying stumps of most coniferous and deciduous trees. In addition, *H. fasciculare* also was chosen for this study because it has shown changes in the phenology and seasonality (refer to chapter 3 and chapter 6) (Gange *et al.* 2007). Furthermore, this fungus was successfully used as an experimental treatment to competitively displace a common fungal disease of conifers*, Armillaria solidipes* from managed coniferous forests (Chapman & Xiao 2000) and this may benefit relevant plants including cedars, pines and spruces. This study ranged within a year (for *H. fasciculare* individuals found

in West Sussex) until 3 y period (for Royal Holloway and Windsor Forest) the period also encompassed a severe drought in certain years, which enables assessment of trends under such unpredictable events. The objectives of this study were i) to document the interaction between *H. fasciculare* pairings in co-culture plates; ii) to determine *H. fasciculare*'s seasonal periodicity; and iii) to provide explanations of the outcome of these interactions.

It was the intention of this study to provide an insight of what scale the population is structured, by asking questions such as how closely related are different individuals within the same population or how big an individual is. The hypothesis of this study was that the same individuals are producing fruit bodies multiple times throughout the year or the following years. This was based upon the fact that multiple fruiting appears to be a recent phenomenon and if there were 'autumn-' and 'spring-fruiting' individuals, this should have been apparent over the entire 58 year of record collection.

6.2 Methodology

6.2.1 Fungal isolates

H. fasciculare samples were collected from three sites in different counties; Windsor, Berkshire (Windsor Forest) (Site 1, Fig. 6.1), Surrey (Royal Holloway College) (Site 2) and Sussex (Wivelsfield RH15 OSS) (Site 3, Fig. 6.3) for three consecutive years, 2010-2012. Spore prints were taken from each sample and transferred to malt extract agar with a sterile blade and cultivated at room temperature until the spores germinated into cottony white mycelium. The coordinates of the location where each fruit body found were also recorded. The total number of fruit body individuals in each cluster found was also counted, to determine whether fungal production varied from site to site. All *H. fasciculare* cultures were maintained on malt-extract agar at room temperature.

6.2.2 Fungal interactions in co-culture

For inoculation, mycelial plugs of 5mm diameter were cut from *H. fasciculare* cultures using an inoculation loop and transferred to a new malt extract agar plate. All possible pair-wise combinations were made by plating the mycelial plugs on the opposite corner of the plate following methods conducted by Sharma *et al.* (2010). Each pair was replicated three times.

Figure 6.1 Study sites at (a) Windsor Forest in Windsor Great Park, b) Royal Holloway College and c) Wivelsfield, West Sussex.

Possible pair-wise combinations were selected based upon the closest location where these individuals were found at different times of the year and between years. Agar plates containing pair combinations were kept at room temperature and sealed with parafilm to avoid contamination. Observations were recorded at 10, 20 and 30 d after plating, similar to the methods applied by Shaw *et al.* (1995) and any interactions observed using a system adapted by Porter (1924). The interaction types were 'deadlock' where a mycelial barrage or clear zone separated the colonies, 'fusion' (self-pairings intermingle to produce uniform mycelial mats) and 'overgrowth' where one mycelium encroached into the other colony, partially or totally taking over its domain. The experiment was terminated when growth of one mycelium interacted with the co-inoculant.

6.3 Results

6.3.1 Interactions in co-culture

All mycelial interactions were completed within 30 days from their first co-culturing. Control co-cultures between study sites demonstrated antagonistic reactions where overgrowth was observed when an *H. fasciculare* individual from Windsor Forest was

interacted with an individual from West Sussex (Figure 6.2a). Similar reactions were also observed for combinations between *H. fasciculare* individuals of Royal Holloway College and West Sussex. Meanwhile, 'deadlock' reaction that indicates neither one mycelium can enter territory occupied by the other was seen in combinations between *H. fasciculare* individual of Royal Holloway and Windsor Forest (Figure 6.2b).

In total, *H. fasciculare* was recorded in nine sites in Windsor Forest during the study period. Meanwhile, seven sites were recorded in Royal Holloway College and one location in Wivelsfield, West Sussex (Table 6.1). Although this study was conducted over three years in a row, not all individuals were found at the same time each year. All records were obtained during the autumn of 2010, summer/autumn of 2011 and the autumn of 2012. No fruit body individuals were found during spring in 2011 and 2012.

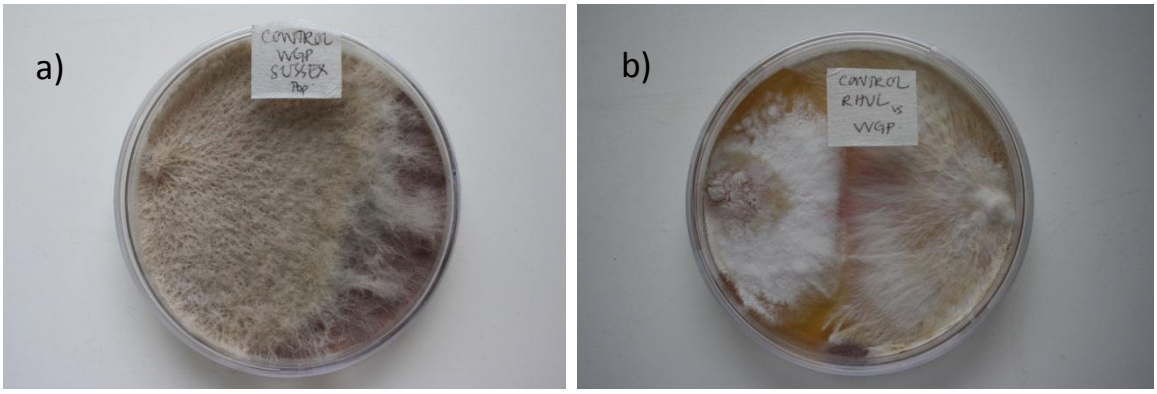


Figure 6.2 Results of the control pairings between three study sites. Overgrowth interactions have been detected in the control pairings of a) WGP – Sussex and b) RHUL – Sussex. Inhibition was detected between RHUL – WGP.

In contrast to WGP and RHUL, *H. fasciculare* individuals in Wivelsfield, West Sussex were only collected during late spring of 2012 and also during autumn of 2012 (Table 6.1). Therefore, pairings between seasons for this site were limited to a year's observation. There were four sites in Windsor Forest that had most records of the fruiting season for three years i.e. Site 1, 6, 7 and 8 while the other study sites showed fewer records. This is because fruit bodies were not found during seasonal forays at the particular sites. For that reason, co-culture method could not be carried out.

Furthermore, of seven sites in RHUL, there were only three sites with records in three consecutive years which are denoted as Site 3, 4 and 6. Three individual combinations for site 3 have shown a fusion interaction throughout the study while pairings for site 4 and 6 have displayed antagonistic reactions of deadlock or contact inhibition reactions, where either mycelium visibly entered the domain occupied by the other, or overgrowth where one mycelium encroached into the other colony, therefore partially or totally taking over its domain in the petri dish. This indicates that several clumps of *H. fasciculare* within the same area appeared to be the same individual while on several other areas, different *H. fasciculare* individuals were found.

The outcome of the cross inoculation method has shown that in most *H. fasciculare* pairings found in WGP study sites have displayed free fusion of mycelia without antagonism in the petri dish, indicating that samples were from the same individual mycelium. The only pairing showing overgrowth in these sites was the individuals that were recorded in study site 8 (N51.4577^{o} W0.6546^{o}) (Figure 6.3). This suggests that all fruiting bodies are of one individual with only one site showed an exception. Similar to WGP, most individuals in RHUL showed fusion reactions in their co-culture plates over three consecutive years. However, *H. fasciculare* individuals found in site 4 (N51.4239^{o} W0.5645^{o}) in 2011 and site 6 (N51.4239^{o} W0.5644^{o}) that were found in both 2011 and 2012 displayed antagonistic reactions towards other individuals in the other sites (Figure 6.4). Besides that, there was one site where *H. fasciculare* was found 200m away from the other individuals in the area which was located at N51.4257^{o} W0.5623^{o} in the 2012 (Figure 6.4). Interestingly, pairwise interactions of *H. fasciculare* individuals between distant sites showed fusion reaction indicating that these individuals were of the same individual even at great distances.

Meanwhile, all co-cultures obtained from West Sussex showed that all paired individuals collected in May and October 2012 from the same tree also have shown fusion reactions entirely (Table 1), showing they were from the same individual. Most WGP pairings from 2010 to 2012 also displayed fusion (75% - 92%) and only 8% -25% of pairings displayed overgrowth interactions. No zones of inhibition were observed in these pair-wise combinations (Figure 6.5).

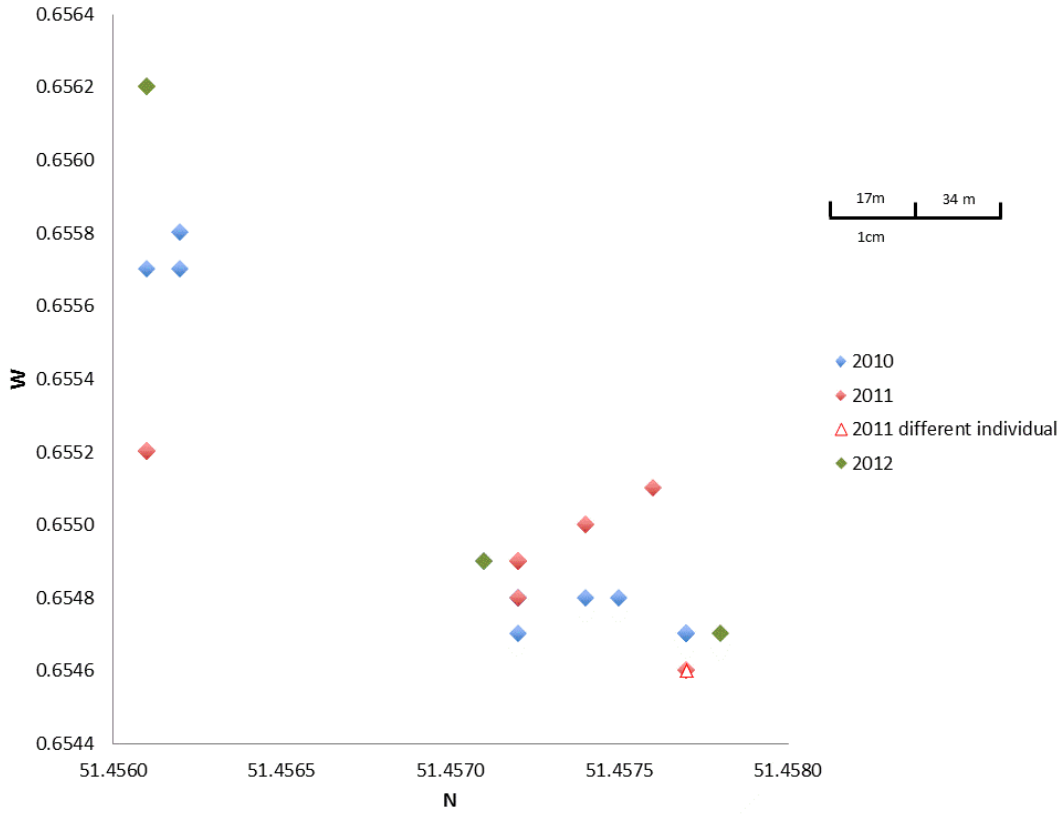


Figure 6.3 Locations of *H. fasciculare* recorded in Windsor Great Park for 2010, 2011 and 2012. Colours indicate which year the samples have been recorded (blue: 2010, red: 2011, green: 2012). Different symbols indicate different individuals.

There were differences in the interactions of *H. fasciculare* that were collected in RHUL. Fusion was the most common interaction (75%) observed in 2010 – 2011 pairings, followed by contact inhibition (22%). However, pairings between 2011 and 2012 and pairings between 2010 and 2012 have shown differences in strength of interactions where fusion, contact inhibition and overgrowth reactions have shown similar proportion in their co-culture interactions (Figure 6.6). There were no inhibitions seen in West Sussex's pairings indicating that all fruit bodies were of the same individual.

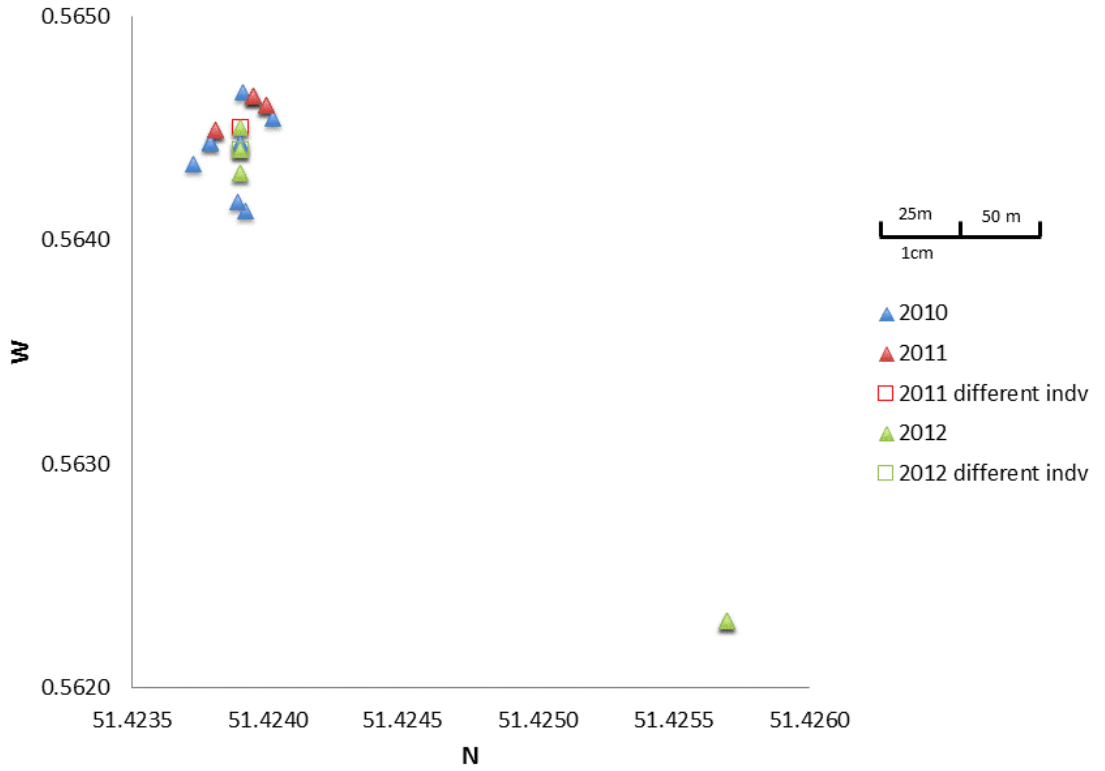


Figure 6.4. Locations of *H. fasciculare* recorded in Royal Holloway College for 2010, 2011 and 2012. Colours indicate which year the samples have been recorded (blue: 2010, red: 2011, green: 2012). Different symbols indicate different individuals.

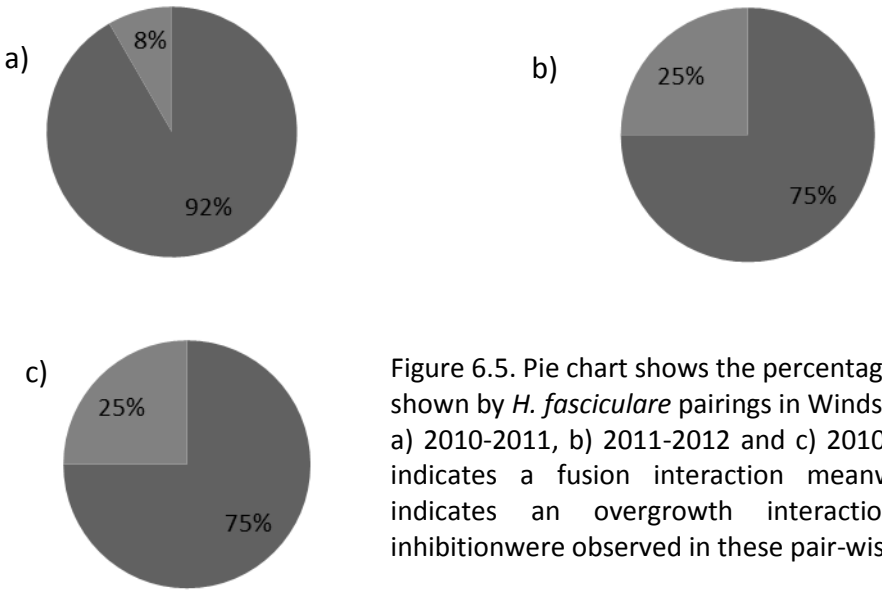


Figure 6.5. Pie chart shows the percentage of interactions shown by *H. fasciculare* pairings in Windsor Great Park for a) 2010-2011, b) 2011-2012 and c) 2010-2012. Darker shade indicates a fusion interaction meanwhile lighter shade indicates an overgrowth interaction. No zones of inhibitionwere observed in these pair-wise combinations.

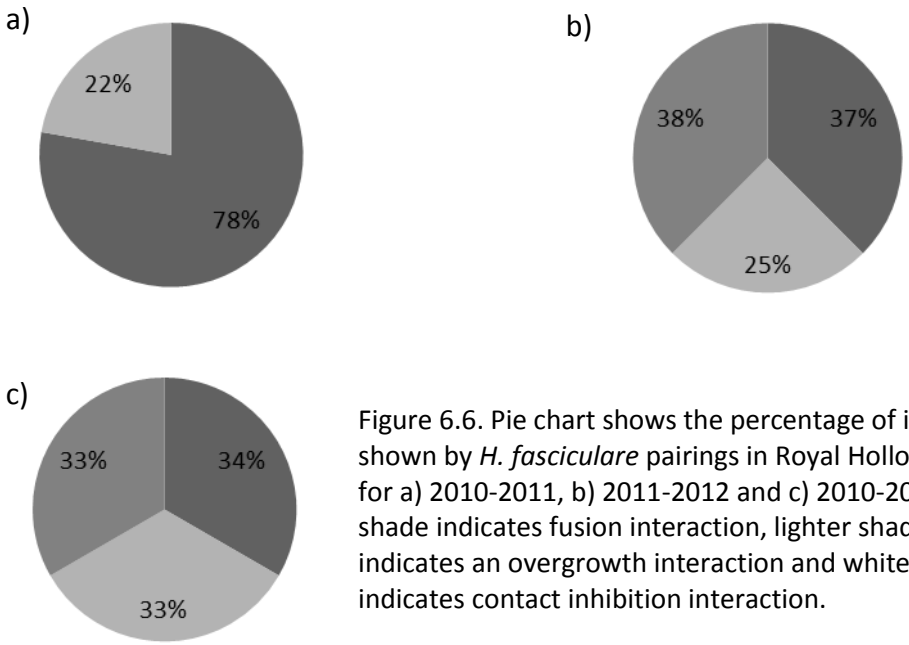


Figure 6.6. Pie chart shows the percentage of interactions shown by *H. fasciculare* pairings in Royal Holloway College for a) 2010-2011, b) 2011-2012 and c) 2010-2012. Darker shade indicates fusion interaction, lighter shade indicates an overgrowth interaction and whiter shade indicates contact inhibition interaction.

Table 6.1. Summary of the *H. fasciculare* interactions in three study sites (WGP = Windsor Great Park; RHUL = Royal Holloway College; Sussex = Wivelsfield, West Sussex). Interactions distinguished were: fusion (F), deadlock (D) and overgrowth (O). (-) indicates that pairing was unavailable as no record obtained on the recorded sites. Top indicates fruit bodies that were collected from the upper part of a tree stump at Wivelsfield study site while bottom indicates fruit bodies that were taken on the lower part of the same tree at Wivelsfield study site.

No.	Sites	Midpoint coordinate	Autumn 2010- Summer/Autumn 2011	Summer/Autumn 2011- Autumn 2012	Autumn 2010- Autumn 2012	2012 Spring - Autumn
1	WGP Site 1	N51.4561° W0.6552°	F	F	F	n/a
2	WGP Site 2	N51.4572° W0.6549°	F	-	-	n/a
3	WGP Site 3	N51.4575° W0.6548°	F	-	-	n/a
4	WGP Site 4	N51.4571° W0.6549°	F	-	-	n/a
5	WGP Site 5	N51.4562° W0.6557°	F	-	-	n/a
6	WGP Site 6	N51.4574° W0.6548°	F	F	F	n/a
7	WGP Site 7	N51.4572° W0.6548°	F	F	F	n/a
8	WGP Site 8	N51.4577° W0.6546°	O	O	O	n/a
9	WGP Site 9	N51.4574° W0.6550°	-	F	-	n/a
10	RHUL Site 1	N51.4238° W0.5644°	F	-	-	n/a
11	RHUL Site 2	N51.4239° W0.5641°	F	-	-	n/a
12	RHUL Site 3	N51.4240° W0.5646°	F	F	F	n/a
13	RHUL Site 4	N51.4239° W0.5645°	F	D	D	n/a
14	RHUL Site 5	N51.4238° W0.5645°	F	-	-	n/a
15	RHUL Site 6	N51.4239° W0.5644°	D	O	O	n/a
16	RHUL Site 7	N51.4239° W0.5647°	F	-	-	n/a
17	Sussex Top		n/a	n/a	n/a	F
18	Sussex Bottom		n/a	n/a	n/a	F

6.4 Discussion

In this co-culture experiment, different interactions in *H. fasciculare* pairings were observed between the three study sites; WGP, RHUL and Sussex. The majority of the fruit bodies found in WGP and Sussex have shown fusion of mycelia without inhibition in co-cultures, suggesting that these fruit bodies were of the same individual. On the contrary, different interactions were seen in RHUL between 2010 and 2012, where some of the fruit body individuals have shown fusion in the co-cultures while some of the pairings displayed antagonistic reactions (either overgrowth or contact inhibition). These data suggest that there were more than one *H. fasciculare* individuals that grew in the same area across the 3 y period. Such results may occur due to the different type of natural management practices in managed and unmanaged semi-natural stands within the district, suggesting an influence of different types of management on the amount and distribution of woody debris i.e. dead wood (Green & Peterken 1997). WGP is part of ancient woodland, renowned for having one of the largest populations of ancient oak and beech trees where less interference is involved. Moreover, the site provides habitats for a range of rare species of invertebrates which include the internationally important violet click beetle *Limoniscus violaceus* and stag beetle *Lucanus cervus* and a rich assemblage of other Red Data book beetles and flies (http://www.english-nature.org.uk/citation/citation_photo/1004110.pdf). The range of provisional Red Data List fungi present includes *Buglossoporus pulvinus, Phelinus robustus, Boletus regius* and *Hericium coralloides* (http://www.english-nature.org.uk/citation/citation_photo/1004110.pdf). In a natural forest like WGP, tree species produce dead wood components that play an essential part in the ecosystem and possess a greater volume which serves as a habitat for wildlife and plays an important part in ecological and geomorphological processes (Harmon *et al*, 1986; Samuelsson *et al*. 1994). Apart from logs, cut stumps (Siitonen *et al.* 2000) are another common above-ground dead wood component that is often overlooked in its contributions towards habitat restoration and fungal development in natural forests. Due to the fact that dead wood i.e. logs and stumps were left to decay naturally on the forest floor without any interference such as grazing and logging for commercial

purposes, this could allow the growth of wood-decay fungi including *H. fasciculare* within the same wood or within the immediate vicinity over time. In addition, active mycelial activity coupled with adequate temperature, resource availability and other factors that enable fungi to grow could possibly encourage the growth of fruiting bodies more than once a year.

Meanwhile, in managed woodland like the study sites in RHUL, dead wood volumes are much smaller than the natural forest due to harvesting and cutting for disposal (Green & Peterken 1997). Location-wise, RHUL woodland which is set within 135 acres (55 ha) of land has been managed by the university for nature conservation purposes (http://www.rhul.ac.uk/aboutus/ourcampus/home.aspx) that involved cutting to restore former species-rich woodland communities for fungi and insects. Therefore, there is a possibility that any coarse woody debris that supported the growth of wood-decay species like *H. fasciculare* in the RHUL woodland may have been transferred from different sites in the area. Moreover, wood where *H. fasciculare* were found may be logs that came from different trees e.g. birch or beech which consequently provide habitats for different individuals.

There were individuals that have been found to fruit within the same sites in different seasons (3 sites in WGP, 1 site in RHUL, 1 site in Sussex), upholding the original hypothesis. Substrate-wise, there is a good chance that a fruit body will grow within the same spot it grew previously, as mycelia that remain hidden within the substrate will only produce new fruit bodies in ideal conditions. In this event, habitat factors including water content of the substratum, effect of atmospheric precipitation, relative humidity, transpiration, indirect and direct action of the wind, temperature and light may play a part in triggering growth of a fruit body (Cooke 1948). Fogel (1976), Hunt and Trappe (1987) and Luoma *et al.* (1991) show that sporocarp biomass production of a single species differs from year to year and weather patterns are likely to be the triggering factor of year-to-year variation (Fogel 1981; Eveling *et al.* 1990). Therefore, this study suggests that some saprotrophic fungi may respond to the variation in the climate conditions that appear in a variety of season over a period of years. In addition, changes in fungal phenology reported by Gange *et al.* (2007) also indicated

that advance fruiting and later appearances of most species in their studies were linked to the preceding increase of temperature and rainfall before the start of the fruiting season in autumn which has led to an expansion of this season. Furthermore, a recent finding by Damialis *et al.* (unpublished 2013) who found a relationship between minimum air temperature and fungal data which led to a discovery of lag-effect or `memory' in fungi has supported the fact that changes in preceding weather affect the current variation of fruiting period. The current study also has shown different trends of fungal fruiting compared to the previous studies. Unlike Luoma et al. (1991), who were not convinced that sporocarps produced in spring may carry over into autumnal collections, results of this study say otherwise. If this activity persists, there is a possibility for the species to have greater expansion in their fruiting seasons.

H. fasciculare individuals that fruit in autumn now can also be found in spring and summer, suggesting that fruiting is based on an active mycelial activity, coupled with variation in seasonal climates. Gange *et al.* (2007) have reported significant numbers of species that previously only fruited in autumn now also fruit either in spring or other times of the year, indicating increased mycelial activity and decay rates in ecosystems in response to changes in spring and summer temperature as well as rainfall. Similar results were also obtained in this study.

In natural environments, it is possible to find different fungal species from different trophic groups of fungi inhabiting the same host/substrates or on a relatively small length of root (Zak & Marx, 1964; Newton 1991). At the same, the mycelia of different species can be found in close proximity to one another (e.g. Marks & Foster, 1967; Danielson & Visser, 1989; Shaw *et al.* 1995). In this situation, the competition for nutrient resources is a common phenomenon that occurs between fungi in order to maintain the survival of their respective species e.g. saprotrophic fungi and ectomycorrhizal fungi (ECM) (Pereira *et al.* 2012). Recent studies have found that *H. fasciculare* has been referred as a highly competitive saprotrophic fungus that could interfere with the growth of mycorrhizal mycelia on tree seedlings (Lindahl *et al.* 2001). Furthermore, it was found that substantial phosphorus (P) could be transferred from several mycorrhizal species (e.g. *Suillus variegatus, Paxillus involutus*) to *H. fasciculare*

or vice versa (Lindahl *et al.* 1999, 2001) and could also include nitrogen (N) transfer (Koide & Kabir 2001; Wu *et al.* 2003,2005). Therefore, there is a possibility that the regular functioning of mycorrhizal species that have weaker combative performance than *H. fasciculare* could be compromised by the presence of this saprotrophic species especially if its mycelia continue to be active for longer periods in the year than before.

The results in this study are preliminary findings which could lead to an extensive study on the intra-specific genetic diversity of saprotrophic fungi and also for future research in order to answer questions such as "over what scale are fungal populations structured", "how big is an individual?", "how closely related are different individuals within the same population, and "how closely related are populations across the UK and Europe?". Simultaneously, further investigations by molecular work including DNA fingerprinting techniques are recommended to investigate whether there is a dichotomy in those individuals that fruit in separate seasons over different spatial scales.

Chapter 7

Co-occurrence patterns of macrofungal species in Windsor Forest: Do mushrooms occur in the same place every year?

7.1 Introduction

There has been interest among mycologists and ecologists in understanding how different ecological factors affect macrofungal community structure and diversity. Factors such as soil chemistry and host specificity are considered important in affecting diversity and community structure of ectomycorrhizal fungi (EMF) (Kennedy 2010), while nutrient resources and climatic factors are expected to affect the maintenance of saprotrophic fungal community structure (Rayner & Todd 1979). There are other factors that also been considered important to have an effect on species interactions in the community that have been discussed in the previous chapters of this thesis (e.g. changes in the fungal phenology in Chapter 3 and changes in fungal-host associations in Chapter 4). Other ecological factors that may have potential effects on the fungal community which have yet to be discovered are the spatiotemporal studies of long-term observations of i) co-occurrence between species of different nutritional modes (e.g. saprotrophic and mycorrhizas) and also ii) seasonal occurrence of species, where off-year gaps in fruiting could be identified and the factors that cause a fungus to fruit could be addressed.

Studies on the co-occurrence of fungi of different nutritional modes are rarely discussed. Most previous studies concentrated on determining existence of interactions among mycorrhizal species by assessing the frequency of co-occurrence of species on colonised roots of a plant (e.g. Urcelay 2002; Koide *et al.* 2005; Mamoun & Olivier 1993 a,b; Wu *et al.* 1999). Moreover, it is also known that specific pairs of mycorrhizal fungi have an exclusive relationship on colonised roots (e.g. Olsson *et al.* 2000). Variation in soil properties such as parent material (e.g. Gehring *et al.* 1998), soil stratification (e.g. Malajkzuk & Hingston 1981; Dickie *et al*. 2002; Landeweert *et al.* 2003; Rosling *et al.* 2003), organic matter content (e.g. Harvey *et al.* 1987), litter

quality (e.g. Goodman & Trofymow 1998; Conn & Dighton 2000), moisture content (O'Dell *et al.* 1999) and fertility (Sagara 1995; Lilleskov *et al.* 2001) are considered as some of the abiotic factors that influence the species composition of ectomycorrhizal fungal communities (Koide *et al.* 2005).

The co-occurrence of mycorrhizal and saprotrophic species within the woodlands is less understood, therefore the original objectives of this study were: 1) to detect presence of co-occurrence among mycorrhiza and saprotophic species and also 2) to determine whether these trends occur more often than expected by chance. However, due to poor seasonal weather conditions (too cold and/or dry) during a large part of this thesis, insufficient data with which to perform the analysis for the co-occurrence patterns was obtained. The objectives were therefore altered and emphasized more towards the determination of the seasonal occurrence of the selected species in the study sites. In addition, studies of co-occurrence require long-term observations and possibly a larger study area in field sites. They also demand a detailed molecular study to detect the presence of any fungal species as hyphae, rather than the fruit body individuals. Moreover, further investigations on competition, parasitism and resource availability also need to be carried out as these factors may have potential to alter the co-occurrences of species.

In studies of macrofungal communities, fruit body records are equally important as molecular techniques in terms of determining changes in the community especially when it involves the occurrence of species. For this, a long-term data based on fruit body records is required to draw any conclusions on the occurrence and behaviour of fruit bodies, as affected by environmental conditions (Straatsma *et al.* 2001). Occurrence normally involves frequency of species, providing another means of evaluating the data, either for interpreting biomass values or as a measure of commonness (Luoma *et al.* 1991). This means that frequency can act as a measure of abundance by showing presence and absence of sporocarps in particular substrates. In vascular plant community studies, frequency traditionally is concerned with the regularity of a species' distribution throughout a community, i.e., homogeneity, and

has been interpreted with caution because variations in plot size, number, and vegetation structure strongly affect the results (Greig-Smith 1983; Luome & *et al.* 1991). Also, similar concerns are applied for fungi, for there are several factors that must be taken into consideration e.g. the number of years of the survey, the protocols for the area to be studied, and the sampling frequency, in order to maintain the quality of sampling (Straatsma *et al.* 2001).

A study conducted by Luoma *et al.* (1991) focusing on the seasonal occurrence of 47 hypogeous species, demonstrated that there are species that show seasonal trends in which most either had spring or autumn production peaks. Besides that, there were also species that showed differences in sporocarp production by habitat. For example, mycorrhizal *Leucogaster rubescens* had peak biomass in dry old-growth habitat while the peak biomass of *Leucophleps magnata* was in habitats other than old-growth. In contrast, another mycorrhizal species, *Rhizopogon vinicolor* was found distributed throughout all habitats in the study. Furthermore, recent findings by Gange *et al.* (2007) have shown that there are significant numbers of UK species that have begun to fruit in spring as well as autumn, suggesting increased mycelial activitiy and increases in decay rates in forests.

In the formation of a fruit body, a primordium, an organ that will develop into a mature fruit body, requires nutrient supplies such as N and $C0_2$ and also ideal conditions such as light, temperature and moisture (Yamanaka *et al.* 2000). However, how much is needed for each factor have yet to be identified. This stage of fruit body development is crucial, as it can ultimately determine abundance and distribution of fruit body individuals in the community. In addition, it is also likely that primordia will fail to develop into fruit bodies if there is a shortfall in certain requirements. Therefore, in this study, I hypothesised that some individuals may exhibit gaps / off-years in their fruiting seasons. This then may lead to the next hypothesis that weather would not be the only factor that triggers the fruiting formation, which suggests that there may be other factors such as light, sudden drop in temperature and rainfall. that encourage mycelia to form primordia thus forming fresh fruit bodies thereafter.

The broad scope of this study allowed the following specific objectives to be addressed: 1) identification of the common species of macrofungi found in Windsor Forest; 2) characterization of the seasonal fruiting aspects of the major species and 3) determination of the seasonal occurrence of the selected species as measured by sporocarp biomass and species frequency.

7.2 Methodology

7.2.1 Study sites

Fruit body surveys were conducted for three consecutive years (2010 – 2012) in the Windsor Forest using random sampling. The study area was closest to where the studies in Chapter 6 were conducted (N51.4555° W0.6540° - N51.4585° W0.6600°) (Figure 7.1).

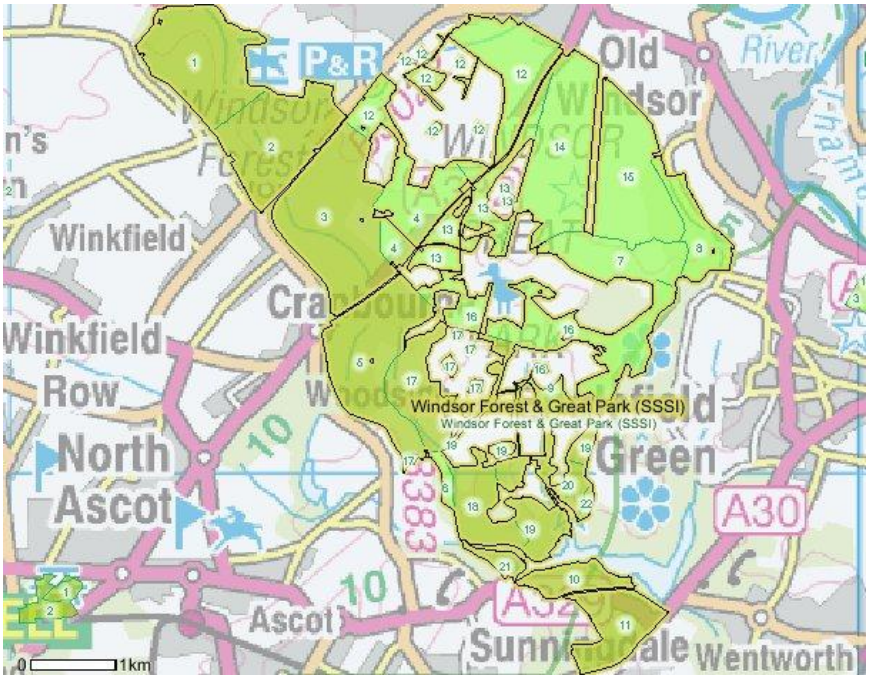


Figure 7.1 Study sites that were located in Sites of Special Scientific Interests in Windsor Forest and Great Park. Source: http://www.natureonthemap.naturalengland.org.uk/map.aspx

The same area was visited at least once every week during the fruiting seasons (March – June and September - November). Several visits were also conducted in summer for

individual comparison in a dry season and on any visit, only fresh fruit body individuals were recorded during the survey; perennial species with permanent fruit bodies were excluded in the recordings. All species that contributed to the 3 y worth of records were gathered and made into a new list. The list contained the species entity, date of collection, number of fruit bodies and grid reference for where the fruit bodies were collected. Later, a summary map was created for each year of records in order to detect presence of species within the same site. Common species were identified based on the occurrence of fruit body individuals in all years of study period and species that were found in two years with one off-year fruiting were also recognised. In total, 2,800 individuals of 18 species were recorded during study period.

7.3 Results

Of 18 species recorded, only seven species were commonly found over the study period (Table 7.1). These were *Amanita muscaria, Hypholoma fasciculare, Laccaria amethystina, Lycoperdon perlatum, Mycena crocata, Russula claroflava* and *Scleroderma citrinum* (Figure 7.2). In terms of occurrence, *H. fasciculare* (N51.4562° W0.6558°) was the only species that appeared at the same exact location every year while the other species were at best only found in two years over the period (Table 7.2) (Figure 7.3). Furthermore, *H. fasciculare* also showed higher abundance than other species as fruit bodies were found in seven scattered areas within the study sites (Table 7.2). *L. amethystina* was the species with the second highest number of individuals (n = 184) followed by *L. perlatum* (n = 131). However, the distributions of these two species were scattered across the study sites and both species failed to fruit in some years (Table 7.2). Several common species in the records only began to fruit in 2011 such as *A. muscaria, R. claroflava* and *S. citrinum* but remained fruiting at the same sites in 2012. In some sites, there were also species that were found in 2010 (Figure 7.4) and 2011 (Figure 7.5) but absent in 2012 (e.g. *H. fasciculare* and *L. amethystina*) (Figure 7.6). Besides that, *H. fasciculare* in two different sites and one of *L. amethystina* were absent in 2011 but appeared in other fruiting years (Table 7.2).

In addition, there were species that did not fruit at the exact same place but appeared within the range of place of origin such as *R. claroflava* (N51.4556° W0.6587) and *M. crocata* (N51.4575° W0.6545°) (Figure 7.5). The first *R. claroflava* fruit body was found in 2011 and appeared in the following year but was found more than 40m away from its original place. Meanwhile, the later fruit body of *M. crocata* in 2012 was found at a distance of 14m from its original place in 2011 (Figure 7.6).

Figure 7.2 Common species in the study sites. From top (left) *A. muscaria* (right) *L. amethystina,* center (left) *L. perlatum* (right) *M. crocata*, bottom (left) *R. claroflava*, (right) *S. citrinum*.

Table 7.1 Macrofungal species found in Windsor Forest between 2010 and 2012. Abbreviations: ecology: m = mycorrhiza, s= saprotrophic. Frequency of occurrence represents the number of fruit body occurrence for each species per year.

Species	Ecology	Total individuals			Frequency of occurrence		
		2010	2011	2012	2010	2011	2012
Amanita citrina	M	13	1		2	1	
Amanita muscaria	M		10	3		3	1
Amanita rubescens	M	16		6	2		1
Boletus chrysenteron	M		3			2	
Boletus edulis	M		23			3	
Clitocybe gibba	S		66	3		3	1
Clitocybe nebularis	S		9	4		1	1
Hypholoma fasciculare	S	149	675	1129	2	4	5
Laccaria amethystina		40	32	112	3	4	3
Laccaria laccata	M			12			2
Lactarius fluens	M	11	8		1	3	
Lycoperdon perlatum	M	2	86	43	1	6	4
Macrolepiota procera	S	1		4	1		1
Mycena crocata	S	1	2	102	1	1	3
Mycena pura	S		14	7		4	3
Russula claroflava	S		3	3		1	2
Russula ochroleuca	M		4	2		3	2
Scleroderma citrinum	M		14	10		6	2
TOTAL		233	915	1440	13	45	31

Table 7.2. Common species occurring in the study sites during study period. Species may occur within the same place or closer to where it was found previously.

Species	Grid reference	2010	2011	2012
A. muscaria	N51.4562° W0.6590°	-	+	+
H. fasciculare	N51.4562° W0.6558°	+	+	+
	N51.4563° W0.6557°	+	-	+
	N51.4568° W0.6548°	+	+	-
	N51.4570° W0.6550°	+	+	-
	N51.4571° W0.6549°	+	-	+
	N51.4563° W0.6587°	-	+	+
	N51.4559° W0.6597°	-	+	+
L. amethystina	N51.4563° W0.6580°	+	+	-
	N51.4561° W0.6556°	+	-	+
	N51.4583° W0.6552°	-	+	+

L. perlatum	N51.4574° W0.6546°	-	+	+
	N51.4569° W0.6546°	-	+	+
M. crocata	N51.4573° W0.6548°	-	+	+
R. claroflava	N51.4556° W0.6587°	-	+	+
S. citrinum	N51.4577° W0.6546°	-	+	+
	N51.4575° W0.6545°	-	+	+

Figure 7.3 a) One of the stumps that hosts *H. fasciculare* in the study site, b) Close-up image of *H. fasciculare* fruit body.

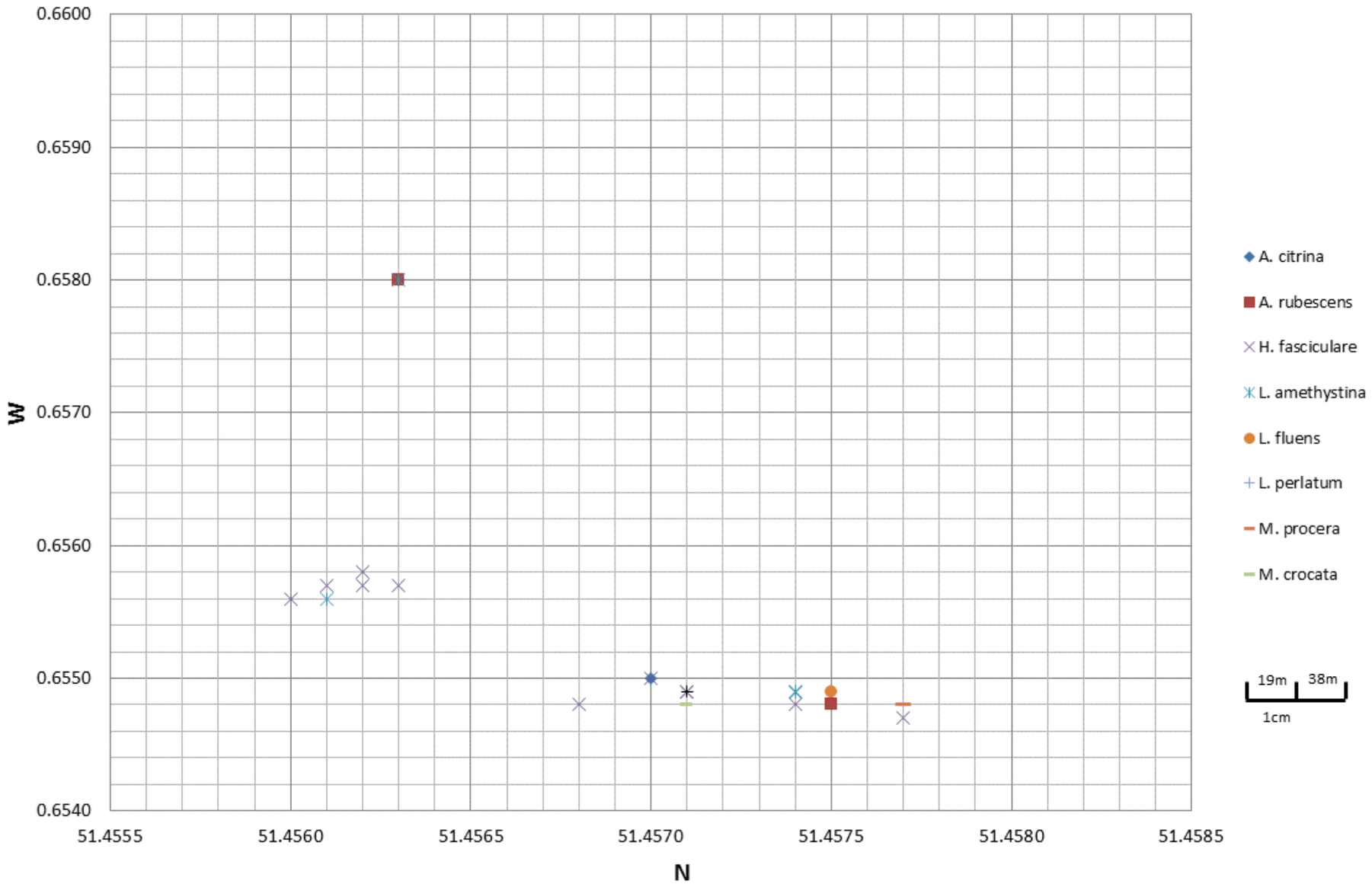


Figure 7.4. Locations of fungal species recorded in Windsor Forest in 2010. Symbols indicate different species. Each square represents 10m x 13m.

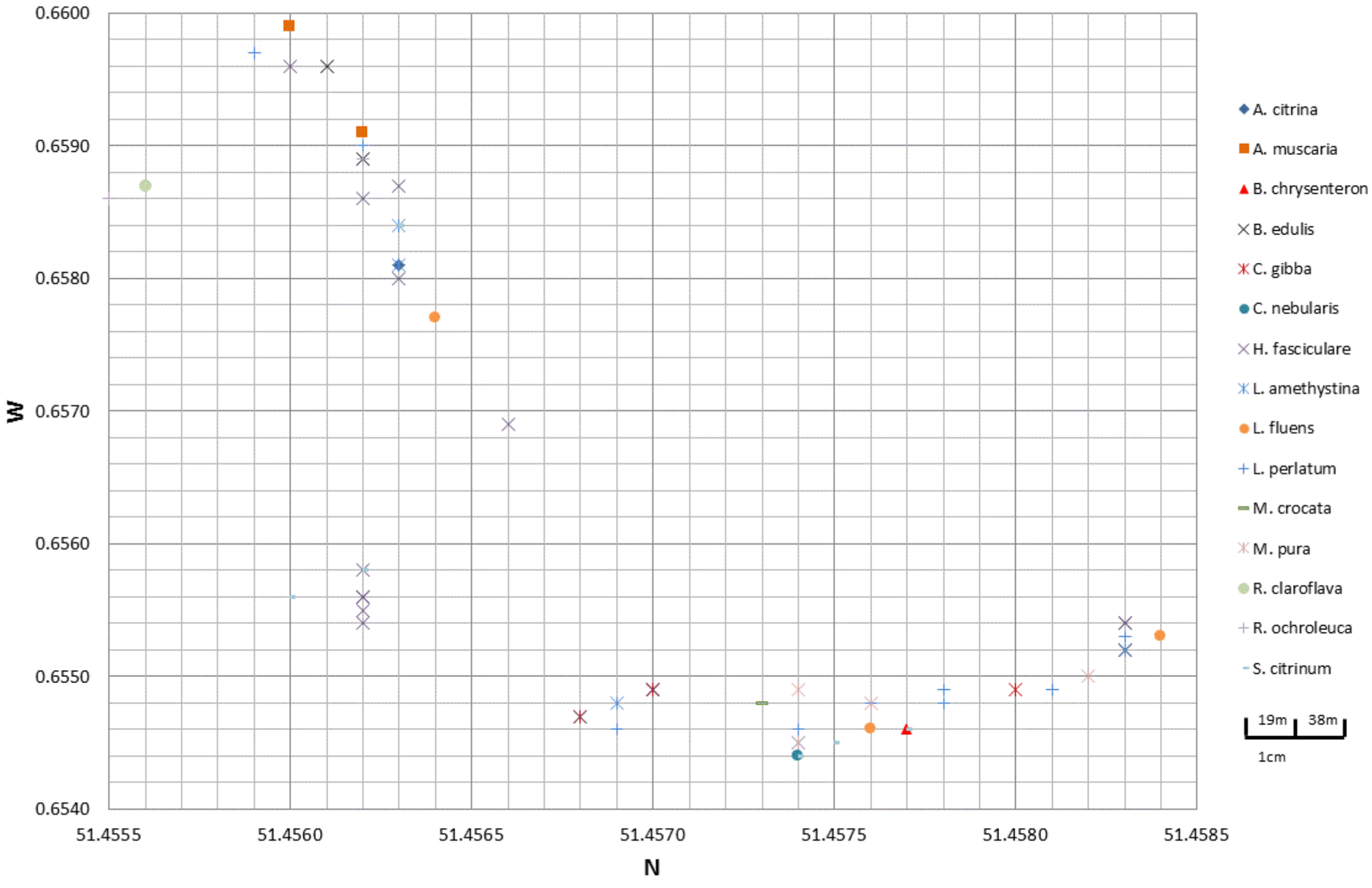


Figure 7.5 Locations of fungal species recorded in Windsor Forest in 2011. Symbols indicate different species. Each square represents 10m x 13m.

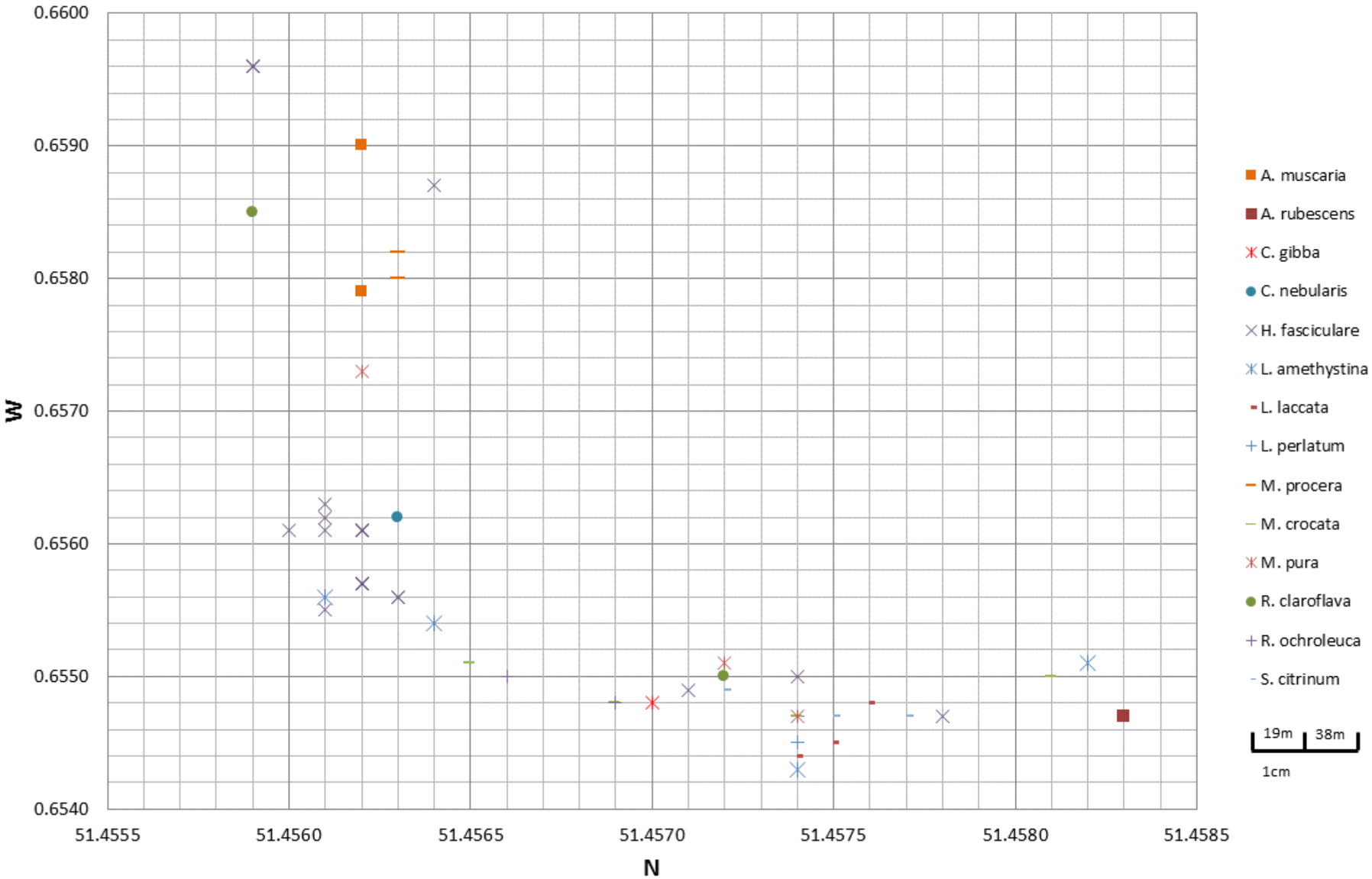


Figure 7.6 Locations of fungal species recorded in Windsor Forest in 2012. Symbols indicate different species. Each square represents 10m x 13m.

7.4 Discussion

The present study provides evidence that majority of common species in the study sites did not fruit every year. Some fruited for two years with no records obtained in the following/previous year while some species displayed a gap between two fruiting years. This begs the question of whether fungi have a resting or an `off-year' period in their fruiting season. This behaviour is not unique to fungi, as it is well known in certain fruit trees. The so-called alternate (or biennial) cycle was defined by Monselise & Goldschmidt (1982) as "an 'on-year' (large yields) followed by an `off-year' (little or no yield) and so on for a sequence of several years. Nowadays, the term "masting" is more applicable to explain this behaviour which has resulted from synchronized variations in reproductive output of individual plants (Schauber *et al.* 2002). This cycle is very common in both deciduous and evergreen fruit trees and is also inherent to polycarpic and perennial plants.

Despite other plant fruiting aspects (e.g. dormancy, time of flower formation, flowering habits, set-abscission relationships, length of fruit development stages) (Monselise & Goldschmidt 1982), masting is a long-term synchronous behaviour that is able to expand over a large scale, up to thousands of kilometres (Koenig and Knops 1998,2000; Kelly *et al.* 2000). Such synchrony may benefit the fitness of individual plants through increased pollination efficiency or satiation of seed consumers (Smith *et al.* 1990; Schauber *et al.* 2002) and populations of those consumers (e.g. grazer animals), as well as other species and ecosystem processes (King 1983; Jones *et al*. 1998, Curran & Leighton 2000, Ostfeld & Keesing 2000). Masting synchrony in plants appears to be affected by weather conditions, especially temperature, which is known to affect photosynthesis and plant growth (Norton & Kelly 1988; Koenig *et al.* 1999, Koenig & Knops 2000). Temperatures during the flowering stage and at the appearance of cone initiation were found to control subsequent seed or flower production in various taxa (e.g. Allen & Platt 1990; Cowan & Waddington 1990; Pucek *et al*. 1993, Kelly *et al.* 2000). Similar relations have been also been found in fungal fruiting, where temperature plays a major role in fruit body production (Pinna *et al.*

2010; Krebs *et al.* 2008). Another similarity between plant masting and fungal `on-and-off-year' fruiting is the ability of fungi to expand their networks. Fungi maintain their survival by colonising new substrates that contain new resources of equivalent size and presumably similar nutritional status as their original 'food base' (Boddy 1999), through mycelial extension. On certain occasions, mycelia may colonise up to thousands of acres in the forest, as shown by *Armillaria ostoyae* in eastern Oregon, US (Hanna *et al.* 2007). Studies have discovered that pairings of fungal samples coupled with DNA fingerprinting have shown that *A. ostoyae* were from the same genetic individual, demonstrating the ecological and evolutionary success of growing with hyphae composed of interconnected cell modules (Busch & Braus 2007).

Alongside these responses, mycelium, which is the essential part responsible for fruit body formation, is another aspect of the fungal lifestyle that must be considered. This often invisible network is always there throughout the year in different substrata (i.e. soil, litters, and logs). Nevertheless, not every mycelium is able to produce primordia, from which a fruit body will develop. However, in stress-free environments, fungal mycelia are still able to expand and colonise away from their original base. For that reason, although any given species may not appear in the exact same location from year to year, other colonies of the same species may fruit elsewhere in the vicinity. As mycelial extent and growth rates will vary, these responses may not be the same for one species or another. This variation in response among different species of fungi suggests that weather may not the only factor that affects the development of the fungal communities. Other factors such as resource availability may be linked to primordia formation. According to Bååth & Sőderstrőm (1979), up to 20% of the total amounts of nitrogen and phosphorus in a boreal forest soil may be incorporated into dead and active fungal mycelium. Moreover, Frankland (1992) in her studies of fungal succession, found a declining number of saprotrophic fungal species when the resource became exhausted. Besides that, laboratory experiments have shown the ability of the mycelium of wood decaying fungi to take up inorganic phosphate from the soil and translocate it to high quality resource units (Boddy 1999; Lindahl *et al.* 2001). Meanwhile, Jonathan & Fasidi (2001) have reported that calcium and

magnesium were the best macro-elements while micro-elements (copper and zinc) enhanced optimum growth of an edible mushroom, *Psathyerella atroumbonata* in laboratory tests.

Apart from resource availability, gases in the atmosphere may be another potential triggering factor for the formation of fruit bodies. Increased CO_2 concentration in the air was found to have a positive effect on mycelial growth in the cultivation of *Pleurotus ostreatus, P. florida* and *P. eryngii* in laboratory experiments (Zadražil 1975). Meanwhile, Wallander & Nylund (1991) who studied the effects of excess nitrogen on ectomycorrhizal mycelium have suggested that nitrogen deposition from the atmosphere may damage the function of mycorrhizal fungi in the environment. They found that mycelial biomass increased rapidly when N was kept low and in balance with other nutrients, but showed no progress of mycelial growth when the N concentration was raised.

Besides nutrient availability and gaseous concentration in the atmosphere, other external factors such as temperature, rainfall, humidity and light conditions also play important roles in deciding whether or not fungi fruit on particular substrates. According to Ugalde (2006), in response to the microenvironment the fungus encounters, this may form an autoregulatory signal, which is a combination of physical and chemical signals that integrate responses of single cells into a higher level of organisation, producing a colony of fruit bodies. Therefore, alterations in any of the external stimuli may affect the signal activity that could affect the formation of the fungal colony.

Furthermore, most species also showed different sequences of fruiting time and frequency of occurrence, indicating that even though a particular year is good for one species to fruit, it does not apply to other species that fruit within the same area. This is most likely due to individualistic responses towards climatic variables that could cause variation in fruiting over years. These findings are not surprising, as similar

responses were previously found within seven common genera in the phenology studies (Chapter 3).

H. fasciculare (located at N51.4562° W0.6558°) was the only species that appeared in the same location every year. However, other *H. fasciculare* fruit body individuals in surrounding areas did not show the same fruiting trend as this individual at this point in space. It is likely that the observed pattern could be due to mycelial activity on particular substrate when the fruit bodies were found.

In addition, chapter 6 of this thesis showed that the majority of *H. fasciculare* fruit bodies found in Windsor Forest over three years (2010 – 2013) were of the same individual. Therefore, it is likely that the *H. fasciculare* fruit body individual that showed continuous fruiting in this study belonged to the same individual network; the same mycelial system that exists within the substrate to produce fruiting bodies on the same substrate over time. In vegetation science, several levels of integration have been applied; the individual, the population, the species, the community (flora), the vegetation unit and the vegetation complex (Wiegleb in press). These levels were categorised into two concepts whereby levels of individual, species and vegetation are often assumed as `real' while the others as `abstract' (e.g. community, ecosystem, flora). The `real' concept represents levels that are based on identity or at least similarity of their components, or, represent the natural environment. Meanwhile, `abstract' denotes likewise abstractions from reality and do not represent nature (Wiegleb in press). These concepts may be analogous to the fungal community development, therefore individualistic reactions displayed by species in this study would represent the 'real' condition of a fungal community structure.

Results from this study were obtained from extensive surveys that have been carried out over three consecutive years. However, some species in this study may be missing within the study period. Such a pattern is common in long-term ecological datasets, therefore, this type of dataset is often cited as 'complex data'. According to Michener et al. (1997), several issues such as missing values, midcourse modification of sampling

or laboratory procedures, addition or deletion of study parameters, personnel turnover, plot or habitat modification by disturbances (natural or anthropogenic) or changing environmental conditions, together with numerous other factors leading to data anomalies are a common situation. Such a pattern will only be seen in local data but would never be seen in a national database. For example, one can find a rare fungal species in a national dataset as anyone in public; from an amateur to an expert mycologist, who is able to access the dataset freely and report any fruit bodies seen within their neighbourhood. However, this situation won't happen in a local dataset as people may only have the species recorded with no intention to seek for one, but may find them accidentally e.g. while walking their dog in the forest or during fungal forays. Moreover, the methods of data collection itself may vary from one study to another and require documentation regarding collection methodologies in practice or new techniques deployed in the field. Such research data require extensive quality assurance and control before preserving them in a public database to avoid bias (Michener *et al.* 1997). Apart from that, the variability of long term fungal datasets also makes them particularly difficult to describe adequately enough for others to use (Karasti *et al.* 2006).

Overall the present study demonstrates that some fungi are able to fruit at the same place over years with the help of several possible environmental factors to trigger their growth. Nevertheless, extensive studies need to be carried in the future with emphasis on the other aspects, e.g. monitoring the quantity of individuals that occur at the same place every year or the abundance of species over years for a better understanding of the way a fungal network can improve the production of fruit bodies in the future.

Chapter 8

General Discussion

Before this research was carried out, very little was known about several various spatial and temporal aspects of fungal community structure, such as fungal fruiting phenology, a species' ability to expand and/or shift their host, seasonal fruiting and also fungal dispersal through time. Therefore, this thesis has uncovered many interesting findings related to the above topics.

The time of appearance of fruit bodies, or phenology, of macrofungi over years is variable among species. Some species are perennial (e.g. *Ganoderma* sp., *Rigidoporus* sp.), and survive on their substrates/hosts over several years while some species are produced seasonally, e.g. many Basidiomycetes. The general phenology observed in this study displayed differences over time in the appearance, disappearance and length of fruiting for different functional groups. Generally, most groups showed earlier onset and later disappearance, which have resulted in an expansion of the overall fruiting season. This observation is also in line with the findings by Gange *et al.* (2007), Mattock *et al.* (2007) and Moore *et al.* (2008) who have demonstrated that the overall autumnal fruiting season in the UK has extended in both directions (i.e appearance and disappearance). Meanwhile, a different phenological pattern was observed in Norway, where the average date of first fruiting for autumnal species tends to be delayed and coupled with later disappearance, has resulted in a compressed fruiting season (Kauserud *et al.* 2008). According to Kauserud *et al.* (2012), this difference is likely to be due to i) geographical variation between the UK and Norway and also ii) differences in the approach that was undertaken to observe the pattern of phenological changes. Previous literature has demonstrated that several external factors including temperature, rainfall, nutrient concentrations, atmospheric gases and soil conditions influence the productivity of fungal fruit bodies (Straatsma *et al.* 2001; Wallenda & Kottke 1998; Klamer *et al.* 2002; Braga-Neto *et al.* 2008). Therefore, it is possible that any changes on these external factors over time may have affected fungal fruiting phenology.

Meanwhile, individualistic responses in fruiting patterns shown by species in most genera suggest that this may result from differences in their biology or any event in the life cycle of a species that is able to accelerate with warming (Thackeray *et al.* 2010). Besides the direct effect of rising temperatures, variation in individual responses of a species in its fruiting aspects could be driven or constrained by changes in the strategy of a species with their resource relations. For example, Dighton *et al.* (1986) indicated that differences in the occurrence of saprotrophic species under different host plants was related to the nature of the resources available in the community, in terms of litter quality (e.g. C:N ratio and polyphenol content, lignin content) as suggested by Cooke & Rayner (1984), Dighton & Mason (1985) and Rayner *et al.* (1985).

Although this research has used data based on one long-term record of fruit body individuals, it has come a long way towards understanding fungal fruiting trends in the UK, allowing us to get a better understanding of the time of fruiting, including the onset and the disappearance of species, and the relationship between these events. Besides that, characterisation of the changes in fruiting will enable us to understand the consequences of global warming, as fungal fruiting is mostly triggered by rising air temperatures. The fact that fungi play critical roles in the forest ecosystem, means that any changes in fungal fruiting may also affect the success of an ecosystem or food chain as changes in fungal appearance could interfere with nutrient recycling processes (for saprotrophic fungi) and also affect symbiotic relationships between mycorrhizal fungi and their host plants. Furthermore, this long term phenology study has also demonstrated that fruiting aspects including the appearance, the disappearance, length of fruiting season and the average date of fruiting for each species have changed and that the apparent changes may indicate real biology changes rather than sampling effects. Therefore, with knowledge of fungal fruiting phenology, we will be able to make predictions about the future health of a fungal community structure.

I have demonstrated that some fungal species have started to show host range expansion and host shift and that saprotrophic fungi were more likely to show greater host range expansion and host shift in comparison to mycorrhizal fungi. Saprotrophic fungi mostly contained wood-decayers and leaf litter decomposers and their occurrence is affected by several factors such as substrate availability, substrate quality and host specificity (Zhou & Hyde 2001) Furthermore, the fact that these fungi are widespread and are able to live upon several hosts, may explain the main finding of this study. Mycorrhizas, on the other hand, live attached to many long-lived coniferous and deciduous plants and form intimate symbiotic relationships with their host plants, making host shift far less likely.

In addition, the host range analysis also displayed similarities with the changes in phenology of some genera that were discussed in *Chapter 3*. Variations in the relationship between host range and fruiting phenology are greater in mycorrhizal fungi while most saprotrophic genera that showed host expansion are likely to demonstrate a longer fruiting season.

Meanwhile, it was demonstrated that fungal species that shifted their hosts also showed changes in their fruiting phenology. Not only are the phenological responses for each genus varied, but there were also differences in responses of species within the same genus, suggesting individualistic reactions, which may be due to changes in their biology caused by climate change. Previous studies have documented that while fungi often have multiple hosts in nature (e.g. Trappe 1962; Bills *et al.* 1986), the factors that determine host preference are unknown. Later, Horton & Bruns (1998) and Kennedy *et al.* (2003) described host preference of several ectomycorrhizal species with more than one host, but failed to document any shifting in fungal host range as no long term records were collected. Therefore, quantitative analyses have been carried out in this study to achieve both aims. Since some fungal species are able to expand and shift their hosts, there might be competition for nutrient resources by different species that may affect individual interactions with the common symbionts including the survival of rare fungal species. Since this study provides first evidence for

the presence of host range expansion and host shift, further attention should be considered by involving molecular tests together with quantitative analysis, to allow a more precise and better understanding of fungal-host associations.

The long term study examining climate effects on fruit body production in this thesis has shown that temperature showed the most influence on phenology compared to rainfall and relative humidity. The lack of relations with rainfall may be due to the inter-annual differences in both climatic factors, suggesting that very fine scales of resolution in time data may be required to show trends.

Meanwhile, most functional groups have demonstrated strong relationships between their phenological aspects (especially i.e FFD and LFD), and temperature variables i.e cumulative maximum and minimum temperatures. However, each group responds in a different way to different temperature attributes. The present study has also found differences in climate-induced responses between mycorrhizal and saprotrophic species in the dataset. These findings, again, may be due to the individualistic reactions meaning that each species has different requirements in their own habitat. Furthermore, all autumnal species that belong to nine functional groups also showed increasing trends in their first fruiting and last fruiting dates with daily heat sums since 1950 until 2000. These findings mirror the changes in British temperatures that have occurred since 1975 (Fitter & Fitter 2002; Gange *et al.* 2007) and indicate that fungi are also affected by the increasing temperature over years. This has resulted in significant changes in the fruiting season of these fungal species over the last 58 y.

Moreover, an exciting discovery was made where almost all functional groups examined in the analyses displayed lag-effect responses or 'long-term memory' with regards to the effect of minimum temperature on the appearance and disappearance of species in each functional group. The minimum temperature in preceding years has affected the present FFD and a similar effect was seen with minimum temperature and fungal disappearance.

Despite changes in the phenology, host association and climatic effects on fungal fruiting, this research also suggested that some individuals are producing fruit bodies more than once throughout the 3 y study period. An inoculation method that was used to observe intra-specific interactions of *Hypholoma fasciculare* in three different sites showed that most fruit body individuals found in Windsor Forest and Sussex were of the same individuals while more than one *H. fasciculare* individual grows in the Royal Holloway College (RHUL) area over the 3 y period. Difference in natural management practices, variation in the climate conditions within the habitat over seasons, active mycelial activity and interspecific competition for nutrient resources are suggested to be the triggering factors for such results. Although this research was not able to find out the scale of the species population and how big is an individual of species within the study area (e.g. Ferguson *et al.* 2003), further extensive studies together with comprehensive methods may promise better understanding on how species productivity could affect the structure of fungal community.

Knowledge about the extent of fungal intraspecific interactions in nature and its role in structuring fungal communities is still poorly understood. This would be improved if more of the following kinds of studies were carried out: i) using molecular techniques to investigate dichotomy in those fruit body individuals that fruit at different times, ii) experimental field studies that involve other common species and different group of fungi such as mycorrhizas, ii) experimental and comparative studies throughout a range of environmental conditions.

The fungal co-occurrence study demonstrated that species tend to have different sequences of fruiting time and frequency of occurrence. Overall, the most common species in the study sites, such as *Amanita* sp., *Boletus* sp., *Clitocybe* sp., *Laccaria* sp., *Lactarius* sp., *Mycena* sp. and *Russula* sp. did not fruit every year. This is most likely due to individualistic responses displayed by each species towards different resource requirements that could cause variation in fruiting over time. This variation in responses among different fungal species demonstrated that climatic conditions (e.g. temperature, rainfall, humidity and light conditions) may not be the only factor that

affect the development of the fungal community, but coupled with other potential factors including resource availability (e.g. soil nutrients) (e.g. Bååth & Sőderstrőm 1979) and gases in the atmosphere (e.g. Wallander & Nylund 1991).

The question of whether macrofungi do have resting periods or an "off-year' to some extent has been answered in this research, however, this aspect is rarely discussed in the literature. Previously, studies that investigated the resting period or dormancy in fungi were examined for spore germination activities of ascomycetous fungi and zygote fungi, where the length of time for maturity varies with the species and spore types (e.g. Gottlieb 1950; Daniels & Graham 1976). However, this has not been discussed extensively in Basidiomycetes, that comprise 30,000 described species, and which include 37% of the described species of true fungi (Kirk et al. 2001), including mushroom, bracket fungi and puffballs.

Furthermore, long term synchronous fruiting behaviour shown by most fungal species in *Chapter 7* of this thesis display similarities with plant masting, where temperature plays the most important role in fruit body production (Krebs *et al.* 2008; Pinna *et. al.* 2010). Furthermore, the ability to expand their networks is also a resemblance between plants and fungi. In order to maintain their survival, some fungi tend to colonise new substrates to obtain new nutritional resources through mycelial extension, and with mycelia growth, rates will vary from one fungal species to another, leading to variation in synchronous fungal fruiting. Nevertheless, extensive studies on co-occurrence patterns need to be carried out in the future with more emphasis on i) monitoring the abundance of fruit body individuals that occur at the same place and ii) applying molecular biology to identify similar individuals that may expand through mycelial system underneath forest floor for species distribution, and ii) long term monitoring of co-occurrence patterns for a better understanding of the way fungal networking systems could improve the fungal community structure.

The question "what makes a fungus fruit" has long been discussed but so far, no one is able to answer this question due to the fact that there is little relevant information for

species other than the few that are cultivated such as *Agaricus bisporus* (button mushroom, white mushroom, brown mushroom or portobello), *Lentinula edodes* (shiitake), *Pleurotus* spp. (particularly P. ostreatus, oyster mushroom) and *Flammulina velutipes* (enoki) (Kalač 2013). Nevertheless, related studies such as the analysis of fruiting patterns combined with other spatial and temporal aspects that have been carried out in the present study might be able to point out some key points that enable us to find the real answer.

The present studies have demonstrated that most spatial and temporal aspects discussed in this research could potentially be influenced by several external factors such as climate (e.g. temperature), humidity, light conditions and gases in atmosphere. Apart from the above factors, internal factors including photosynthetic activities by host plants also correspond with the adjustment of the phenology of mycorrhizal fungi whereby large amount of assimilates from host plants can exceed the storage of capacity of mycelia in mycorrhizal fungi, which route the excess to fruiting bodies during the host plant growing season (Högberg *et al.* 2010; Högberg *et al.* 2001). Besides that, the fungal mycelium is also responsible for obtaining nutrient sources, whether from the host plant (mycorrhizas) or by inhabiting new substrates (saprotrophic fungi) and is a major component of fungi growth, because this network determines whether primordia have enough requirements to produce the fruit body of a fungus.

It is not surprising that in order to fruit, a fungus may require various sources at the same time, both internal and external resources. Externally, autumnal fungal fruiting is probably triggered by the sudden drop of temperature approximately at the beginning of September as reported by Straatsma *et al.* (2001). Meanwhile, annual rainfall that fluctuates over years with the occurrence of lagged responses (i.e. time of fruiting that depends on climatic conditions from the preceding year), which were obtained from the present study may also contribute to the formation of fungal fruit body. Apart from that, other factors that should be considered are regional cumulative precipitation (Bűntgen et al. 2012), various resource availability i.e. preceding

assimilate fluxes resulting from photosynthesis from host plants to fungi for mycorrhizal species (Lamhamedi *et al.* 1994) and availability of decomposing substrates for saprotrophic fungi (Sato *et al.* 2012). Therefore, overall, one can conclude that climate is not the only key determinant of the appearance and disappearance of fungal fruit bodies.

Appendices

Species in the dataset

a) Grass

Agaricus arvensis
Agaricus bisporus
Agaricus bitorquis
Agaricus campestris
Agaricus xanthodermus
Agrocybe praecox
Bovista plumbea
Calocybe gambosa
Calvatia excipuliformis
Calvatia utriformis
Clavaria vermicularis
Clavulinopsis corniculata
Clavulinopsis fusiformis
Clitocybe dealbata
Clitocybe rivulosa
Conocybe lactea
Conocybe tenera
Coprinus comatus
Coprinus plicatilis
Entoloma incanum
Entoloma sericeum
Entoloma staurosporum
Hygrocybe ceracea
Hygrocybe conica
Hygrocybe miniata
Hygrocybe pratensis
Hygrocybe psittacina
Hygrocybe virginea
Langermannia gigantea
Lepista saeva
Leucoagaricus leucothites
Lycoperdon lividum
Lyophyllum connatum

Macrolepiota procera
Marasmius oreades
Melanoleuca vulgaris
Morchella esculenta
Mucilago crustacea
Mycena aetites
Mycena flavoalba
Omphalina ericetorum
Panaeolina foeniscii
Panaeolus ater
Psathyrella atomata
Psathyrella conopilea
Vascellum pratense
Volvariella speciosa

b) Mycorrhizal coniferous

Hygrophorus hypothejus
Lactarius deliciosus
Lactarius hepaticus
Lactarius rufus
Russula emetica
Russula sardonia
Suillus bovinus
Suillus grevillei
Suillus luteus
Tricholoma argyraceum
Tricholoma terreum
Xerocomus badius

c) Leaf litter

Agaricus haemorrhoidarius
Agaricus silvicola
Clitocybe clavipes
Clitocybe flaccida
Clitocybe fragrans
Clitocybe geotropa
Clitocybe gibba
Clitocybe nebularis
Clitocybe odora

Clitocybe phyllophila
Clitocybe vibecina
Clitopilus prunulus
Collybia butyracea
Collybia confluens
Collybia dryophila
Collybia maculata
Collybia peronata
Coprinus picaceus
Coprinus silvaticus
Hemimycena cucullata
Lepiota aspera
Lepiota castanea
Lepiota cristata
Lepista nuda
Lycoperdon molle
Lycoperdon nigrescens
Lycoperdon perlatum
Macrocystidea cucumis
Marasmius cohaerens
Marasmius epiphyllus
Marasmius wynnei
Mutinus caninus
Mycena capillaris
Mycena metata
Mycena pelianthina
Mycena polyadelpha
Mycena rosea
Mycena vitilis
Peziza repanda
Phallus impudicus
Psathyrella obtusata
Pseudoclitocybe cyathiformis
Setulipes androsaceus
Stropharia aeruginosa
Tubaria dispersa
Tubaria furfuracea
Tylopilus felleus
Xerula radicata

d) Mycorrhizal deciduous

Amanita citrina
Amanita echinocephala
Amanita fulva
Amanita muscaria
Amanita pantherina
Amanita rubescens
Amanita strobiliformis
Amanita vaginata
Amanita virosa
Boletus edulis
Boletus erythropus
Boletus luridus
Cantharellus cibarius
Cantharellus tubaeformis
Cortinarius alboviolaceus
Cortinarius anomalus
Cortinarius elatior
Cortinarius hinnuleus
Cortinarius sanguineus
Entoloma neglectum
Geastrum fimbriatum
Geastrum triplex
Hebeloma crustuliniforme
Hydnum repandum
Hygrophorus eburneus
Inocybe asterospora
Inocybe bongardii
Inocybe geophylla
Inocybe lacera
Inocybe lilacina
Inocybe napipes
Inocybe patouillardii
Inocybe pyriodora
Inocybe rimosa
Inocybe umbrina
Laccaria amethystina
Laccaria laccata
Lactarius blennius
Lactarius fuliginosus

Lactarius glyciosmus
Lactarius piperatus
Lactarius pyrogalus
Lactarius quietus
Lactarius subdulcis
Lactarius tabidus
Lactarius torminosus
Lactarius turpis
Lactarius vellereus
Lactarius zonarius
Leccinum scabrum
Leccinum versipelle
Paxillus involutus
Russula adusta
Russula aeruginea
Russula atropurpurea
Russula betularum
Russula claroflava
Russula cyanoxantha
Russula delica
Russula fellea
Russula foetens
Russula fragilis
Russula heterophylla
Russula lepida
Russula mairei
Russula nigricans
Russula ochroleuca
Russula virescens
Russula xerampelina
Tricholoma album
Tricholoma fulvum
Tricholoma sulphureum
Tricholoma ustale
Xerocomus chrysenteron
Xerocomus subtomentosus

e) Live leaves

Coleosporium tussilaginis
Kuhneola uredinis

Melampsora populnea
Melampsorella symphyti
Microsphaera alphitoides
Puccinia lagenophorae
Puccinia malvacearum
Puccinia punctiformis
Puccinia sessilis
Uromyces ficariae
Uromyces muscari

f) Needle litter

Agaricus sylvaticus
Chroogomphus rutilus
Clitocybe brumalis
Cystoderma amianthinum
Hygrophoropsis aurantiaca
Macrolepiota rhacodes
Mycena acicula
Mycena leptocephala
Mycena pura

g) Manure

Bolbitius vitellinus
Coprinus ephemerus
Coprinus lagopus
Coprinus niveus
Panaeolus campanulatus
Panaeolus semiovatus
Panaeolus sphinctrinus
Poronia punctata
Psilocybe coprophila
Stropharia semiglobata

h) Soil

Aleuria aurantia
Clavulina cinerea
Clavulina cristata
Clavulina rugosa

Coprinus atramentarius
Cystolepiota sistrata
Helvella crispa
Helvella lacunosa
Leotia lubrica
Peziza badia
Scleroderma areolatum
Scleroderma verrucosum
Tarzetta catinus
Tephrocybe atrata

i) Living trees

Armillaria mellea
Collybia fusipes
Daedaleopsis confragosa
Fistulina hepatica
Ganoderma applanatum
Gymnopilus junonius
Inonotus hispidus
Laetiporus sulphureus
Meripilus giganteus
Oudemansiella mucida
Phaeolus schweinitzii
Pholiota aurivella
Pholiota squarrosa
Piptoporus betulinus
Sparassis crispa

j) Dead wood

Ascocoryne sarcoides
Auricularia auricula-judae
Auricularia mesenterica
Bisporella citrina
Bjerkandera adusta
Bulgaria inquinans
Byssomeruliopsis corium
Calocera cornea
Calocera viscosa
Ceratiomyxa fruticulosa
Chlorociboria aeruginascens

Chondrostereum purpureum
Coprinus disseminatus
Coprinus micaceus
Crepidotus mollis
Crepidotus variabilis
Cudoniella acicularis
Dacrymyces stillatus
Daedalea quercina
Daldinia concentrica
Diatrype disciformis
Diatrype stigma
Diatrypella favacea
Enteridium lycoperdon
Exidia glandulosa
Exidia thuretiana
Flammulina velutipes
Fuligo septica
Grifola frondosa
Gymnopilus penetrans
Heterobasidion annosum
Hymenochaete corrugata
Hymenochaete rubiginosa
Hyphodontia barba-jovis
Hyphodontia sambuci
Hypholoma fasciculare
Hypholoma sublateritium
Hypoxylon fragiforme
Hypoxylon fuscum
Hypoxylon multiforme
Kretzschmaria deusta
Kuehneromyces mutabilis
Lachnum virgineum
Lacrymaria velutina
Lenzites betulina
Lycogala epidendrum
Lycoperdon pyriforme
Marasmiellus ramealis
Marasmius rotula
Megacollybia platyphylla
Micromphale foetidum

Mollisia cinerea
Mycena adscendens
Mycena alcalina
Mycena arcangeliana
Mycena clavularis
Mycena galericulata
Mycena galopus
Mycena haematopus
Mycena hiemalis
Mycena inclinata
Mycena olida
Mycena polygramma
Mycena rorida
Mycena speirea
Nectria cinnabarina
Neobulgaria pura
Orbilia xanthostigma
Panellus mitis
Panellus serotinus
Panellus stipticus
Paxillus atromentosus
Peniophora lycii
Peniophora quercina
Phellinus ferreus
Phellinus ferruginosus
Phlebia radiata
Phlebia tremellosa
Pleurotus cornucopiae
Pleurotus ostreatus
Pluteus cervinus
Pluteus cinereofuscus
Pluteus romellii
Pluteus salicinus
Pluteus thomsonii
Pluteus umbrosus
Poculum firmum
Polyporus badius
Polyporus brumalis
Polyporus squamosus
Polyporus varius

Postia caesia
Postia stiptica
Psathyrella candolleana
Psathyrella gracilis
Psathyrella hydrophila
Psathyrella multipedata
Pseudohydnum gelatinosum
Psilocybe crobula
Ramaria stricta
Resupinatus applicatus
Sarcoscypha austriaca
Schizopora paradoxa
Scutellinia scutellata
Sebacina incrustans
Stemonitis fusca
Stereum gausapatum
Stereum hirsutum
Stereum rugosum
Stereum sanguinolentum
Thelephora penicillata
Thelephora terrestris
Trametes gibbosa
Trametes hirsuta
Trametes versicolor
Trechispora mollusca
Tremella foliacea
Tremella mesenterica
Trichaptum abietinum
Tricholomopsis rutilans
Tubaria conspersa
Tubifera ferruginosa
Vuilleminia comedens
Xylaria carpophila
Xylaria hypoxylon
Xylaria longipes
Xylaria polymorpha

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