FUNGAL ECOLOGY XXX (2013) 1–14

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Climate variation effects on fungal fruiting

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ARTICLE INFO

Article history:
Received 21 May 2013
Revision received 28 October 2013
Accepted 28 October 2013
Available online ■
Corresponding editor:
Erik Hobbie

Keywords:
Basidiomycetes
Climate
Databases
Fruiting phenology
Host change

ABSTRACT

Earth's climate is changing. Effects of climate change on fungal distribution and activity are hard to predict because they are mediated in many different ways, including: fungal physiology, reproduction and survival, host physiology, spatial and temporal distribution of hosts, resource availability and competition. Currently it is hard to monitor such effects on fungal mycelium in the field, but fruit bodies provide a useful surrogate. Here we review the effects of climate change on phenological changes in fungal fruiting and fruit body yield, and on fungal hosts and distribution, particularly of saprotrophic and ectomycorrhizal basidiomycetes. We report that fruiting phenology is changing in many European countries: on average, the fruiting season is extending, though for some species it is contracting; different species and ecological groups behave differently; time of fruiting depends on geographical location; some fungi now fruit early in the year as well as in autumn, and spring fruiting is getting earlier; some fungi appear to be changing hosts; fruit body yields vary dramatically from year to year; the amount, duration and frequency of fruiting are influenced by numerous environmental factors. We also consider difficulties in assessing phenological and distributional data, and provide suggestions for future research directions at the interface of laboratory experiments and field observations, including molecular approaches and monitoring systems.

Introduction

Earth's climate is changing. By 2100, the atmospheric concentration of CO_2 is predicted to rise to 540–970 ppm above the current concentration. Together with other greenhouse gases such as CH_4, this will lead to a predicted global increase of 1.1–6.4 °C, depending on different models used and global region (IPCC, 2007). Further, the severity and frequency of extreme events are expected to increase. Even more important for terrestrial ecosystem functioning and productivity are

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1754-5048/$ – see front matter
http://dx.doi.org/10.1016/j.funeco.2013.10.006

Please cite this article in press as: Boddy L, et al., Climate variation effects on fungal fruiting, Fungal Ecology (2013), http://dx.doi.org/10.1016/j.funeco.2013.10.006

predicted alternations of the hydrological cycle. Ecological consequences of shifts in temperature means, precipitation and drought spells have been widely reported at spatio-temporal scales, including changes in length and timing of the growing season (Parmesan and Yohe, 2003; Walther, 2010). Unravelling these effects of climate variation on fungal distribution and fruiting is a major current challenge.

In terrestrial ecosystems, almost all organisms ultimately rely both on decomposer fungal communities to recycle carbon and mineral nutrients, and on mycorrhizal fungi to supply plants with nitrogen, phosphorus and water. Understanding the responses of the lowest trophic level is critical if we are to adapt to and mitigate the ecological consequences of climate change (Walther et al., 2002, Walther, 2010). Further, it is well accepted that climate change also affects fungal pathogens of plants, and such effects must be understood and managed particularly with respect to consequences for human food supply (Chakraboty and Newton, 2011). Similarly, fungal diseases of animals (both vertebrates and invertebrates) are influenced, with possible consequences for insect pests, as well as more general wildlife and human populations (Fisher et al., 2012). Fungi are also important components of the diet of many animals including soil invertebrates and small mammals (Boddy and Jones, 2008).

Though the visible macroscopic fruit bodies have economic value as aesthetic components of the natural environment and as a food crop in the case of edible species, it is the mycelium hidden within the substratum from which the fungus obtains its nutrition that is key to the roles that (non-lichenised) fungi play in ecosystem function. Quantifying the abundance of these organisms in bulky, opaque substrata such as leaf litter, soil or wood remains a major challenge (Baldrian et al., 2013). Surrogates for the presence and activity of fungi are, therefore, usually used. In the case of plant and animal pathogens the presence of disease is the main surrogate (e.g. Fisher et al., 2012). For saprotrophic and ectomycorrhizal macrofungi – the main focus of this review – recording fruit bodies can provide a valuable surrogate, though while absence of fruit bodies cannot be taken as absence of mycelia, their presence can be used to infer mycelial activity (e.g. Watling, 1995). In the future, molecular approaches are likely to allow large-scale direct detection of fungal communities in soils (e.g. Clemmensen et al., 2013).

Effects of climate change on fungal distribution and activity are hard to predict because they are mediated in many different ways, including: fungal physiology, reproduction and survival, host physiology, spatial and temporal distribution of hosts and resource availability, and outcome of competitive interspecific interactions. Moreover, the effects of temperature, water and CO_2 and a combination of these are complex, e.g. moisture content effects may differ depending on temperature, and affect different physiological processes and life-style traits differently (Boddy, 1984).

Influences of climatic variables on fungal physiology *in vitro* are well-documented. Metabolic activity increases, for example, with rising temperatures, due to effects on enzyme-catalysed reactions, up to an optimum after which it decreases, due to denaturing of proteins etc., i.e. reactions are often non-linear. Under temperate and boreal conditions, temperatures above the optimum rarely occur except in locations exposed to direct insolation, but nearer the equator inhibitory temperatures might be more common. Moisture inhibits activity when there is both too little and too much: low water potential causes difficulties in taking up and retaining water, and of enzyme function; high water content exerts effects by decreasing rate of diffusion of O_2 to hyphae and of CO_2 away from hyphae (Boddy, 1986). The effect of high water content is less at cold temperatures than at warmer temperatures, because metabolism is slower at lower temperatures. Though elevated CO_2 affects fungal physiology, the predicted atmospheric increases are unlikely to have little direct impact on mycelium in soil and litter where levels are already above ambient. However, mycorrhizal fungi can be affected indirectly via effects of elevated CO_2 on plant physiology and on fixed carbon entering soil from roots (Treseder, 2004). Despite this understanding of ecophysiology, it is extremely hard to extrapolate from knowledge of individual processes, in individual species, in constant conditions to effects of climate change on fungi living in mixed communities in the field, and exposed to continually fluctuating environments. That dramatic changes occur, as a result of fluctuating climate, is evident from long-term datasets on the timing of fruiting and on fruit body productivity of macrofungi in the field, as described below.

Here we review the effects of climate change on phenological changes in fungal fruiting and fruit body yield, fungal ecology, and to a lesser extent life-history and distribution. Difficulties in assessing phenological and distributional data are considered, and suggestions provided for future research directions at the interface of laboratory experiments and field observations, including molecular approaches and monitoring systems.

Considerations when assessing phenological changes

This overview synthesises information from a variety of different types of datasets (Table 1), from different geographical areas, and covering different, sometimes overlapping, groups of species. These datasets range between relatively systematic, localised surveys of relatively small areas (e.g. Gange et al., 2007; Egli et al., 2006; Büntgen et al., 2012b; Sato et al., 2012) to national database collections (e.g. Kauserud et al., 2008, 2012) (see Supplementary material 1 for details of some long-term datasets). Each approach has different advantages and disadvantages (Table 2) associated with biases. Localised survey datasets tend to be higher quality but not very common. Even when closely related statistical approaches are used to assess patterns, results may differ and be interpreted differently (Gange et al., 2013; Kauserud et al., 2013), not least because of scale issues. Datasets from localised surveys will be more affected by local conditions, while countrywide datasets may better reveal more general patterns (Delisle et al., 2003). However, geographic differences in seasons will influence phenology and possibly phenological changes. Further, unbalanced numbers of records across regions may lead to spurious effects. Therefore, direct statistical comparison of local datasets with national datasets is urgently needed, and this is the subject of our current research.

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Table 1 – Long-term dataset analyses of climate change effects on basidiomycete phenology

Location	Type of dataset	Ecological group	Fruiting period	Major findings	References
Switzerland, La Chanéaz in west of country[a]	75 ha forest plot, 1975–1999.	Saprotrophic and mycorrhizal	Autumn	Fruiting was correlated with Jul. and Oct. temperature. Productivity was correlated with precipitation during Jun. to Oct.. Saprotrophic and mycorrhizal species behaved similarly.	Straatsma et al., 2001
	75 ha forest plot, 1975–2006.	Mycorrhizal: 273 species	Autumn	Mean fruiting date 10 days later post- than pre-1991; number of fruit bodies has doubled.	Büntgen et al., 2012
UK, 30 mile radius centred around Salisbury in southern England[a]	Records made several times a week, every week of every year 1950 – present. Identity of each fruit body seen was recorded.	Saprotrophic and mycorrhizal	Autumn	Fruiting season has extended from 33 d in the 1950's to 75 d in 2007.	Gange et al., 2007
		Mycorrhizas	Autumn	Last fruiting date of fungi associated with deciduous trees is now later than in the 1950's, while that with conifers is little changed.	
		Saprotrophic	Spring	Many now fruit in the spring as well as the autumn.	
			Spring	Fungi that fruit in the spring now fruit earlier.	Mattock et al., 2007
		Saprotrophic	Autumn	Time of fruiting of early and late autumn species was related to temperature and rainfall, but in different ways.	Moore et al., 2008
		Saprotrophic	Autumn	Host range of *Auricularia auricula-judae* has increased; fruit bodies are now produced earlier and fruiting extends longer.	Gange et al., 2011
Norway[a]	Mycarium records, 1940–2006.	Saprotrophic and mycorrhizal	Autumn	Mean fruiting delayed 13 d since 1980. Early fruiting species delayed more than late fruiting species. Earlier fruiting in northern and more continental areas.	Kauserud et al., 2008
Norway[a], UK[a]	Mycarium and national database records.	Saprotrophic and mycorrhizal: 34 species	Spring	18 days earlier fruiting in 2007 than 1960, correlated with higher winter temperatures. Climate in previous year also affects fruiting timing. Fruiting highly correlated with geographic location.	Kauserud et al., 2010
Austria, Norway[a], Switzerland[a], UK	Mycarium and national database records.	Saprotrophic and mycorrhizal: 486 species	Autumn	Fruiting season widening between 1970 and 2007. Mean annual fruiting date now later. End of fruiting season now later, particularly in the UK.	Kauserud et al., 2012
Norway[a]	Mycarium records.	Mycorrhizas: nine species	Autumn	Temperature is a major determinant of distribution.	Wollan et al., 2008
China, Yunnan Province	1 ha forest, 2 000–2010, dates of emergence of each individual fruit body were recorded.	Mycorrhiza: *Tricholoma matsutake*	Jun.–Oct.	Fruiting started later in 2010 than 2000. Drought in 2010 delayed fruiting considerably, but there was doubled fruit body productivity.	Yang et al., 2012
Japan, Higashiyama hills eastern Kyoto city	Monthly sampling 1982–2011. Long-term fixed point recording: complete species census along a set 2 km route.	Saprotrophic and mycorrhizal: 668 species		Analysed richness (number of species fruiting at each sampling) of epigeous fungi. Greater ectomycorrhizal richness associated with higher temperatures and higher monthly accumulated rainfall. Overall litter decay fungi were affected similarly, but effects of temperature and rainfall varied between genera. Temp and rainfall affected different genera off wood decay fungi differently.	Sato et al., 2012
Michigan, USA	Mycarium records.	Saprotrophic and mycorrhizal: 274 species	Autumn	Autumn fruiting is later in warmer, drier years.	Diez et al., 2013

[a] Further details about these datasets are provided in Supplementary Table 1.

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Table 2 – Comparison of features of databases of high quality, local survey records with national mycarium records

	Local survey records, intensively sampled	National database records
Collectors/recorders	Few	Many
Inconsistencies in identification and species concepts	Few	Potentially many
Inconsistencies in taxonomy	Few	Potentially many, e.g. a species called by several different names and then treated as several different species[a]
Inconsistencies in sampling intensity	Few	Different for different regions and for different times
Ways of recording time	Standardised	Variable; some records may be as year, month or day
Resolution of position	Relatively standardised	Variable; ranging amongst county, vice-county (UK), approximate descriptions, or geo-referenced (to different levels of accuracy)
Sampling intensity	Relatively consistent	Variable in space and time
Accuracy with which first and last fruiting dates of species can be determined	High	Low
Spatial coverage	Narrow	Broad
Temporal coverage	Often short-term[b]	Often long-term
Spatial scale	Small area	Countrywide
Effects of changing land use	Marked	Less marked
Bias towards certain taxa	Relatively unbiased if all taxa are recorded, though some datasets specialise in specific ecological or taxonomic groups	Often biased against common taxa, since there is a tendency for individuals to report rarer or interesting species

[a] Some database managers try to standardise records.
[b] But some extend for many years (see Table 1).

Trends can occur in all types of datasets as a result of changes, often unrealised, in sampling over time, and it can be very difficult to separate these changes from actual phenological changes over time. Differences in sampling intensity are a major issue, particularly in national datasets where number of annual records tends to be much higher in recent times. This systematic change in the number of records may alone lead to apparent shifts in, for example, the start and end of the fruiting season (see below). Changes in sampling behaviour over time, e.g. relatively different numbers of records sent by individuals recording one or a few selected taxa compared with forays that report all taxa seen, may be particularly problematic for national datasets. The behaviour of field workers, their expertise, interest and emphasis may change over time (Heilmann-Clausen and Læssøe, 2012). For example, when people start to really look for species, they start to find them, e.g. the Burgundy truffle in Germany (Stobbe et al., 2012). Other confounding effects with time occur as a result of land use and landscape change (e.g. woodlands maturing; e.g. Gillet et al., 2010), changes in pollution (e.g. general and localised decrease in SO_2 and increase in nitrogen inputs), as well as climate change. We are dealing with 'a moving target' of where and what we are recording.

Comparison of datasets from different countries and comparison of different analyses can yield yet more problems, including: (1) Different taxonomies: species A in one country may be called species B in another, or may even be divided into sub-species. (2) The starting date of each year is often different and arbitrarily set, e.g. to 1 Jan. (Gange et al., 2007; Kauserud et al., 2008) or 1 Mar. (Kauserud et al., 2012); the main reasons for not starting at the beginning of the calendar year are (i) to optimise the distribution of time points, e.g. to attain normality or (ii) to choose a biological cut off e.g. the end of winter. It is often necessary to consider whether records in the tail of the distribution are exceptionally early or exceptionally late. (3) Use of different response variables such as percentiles or actual date for start and end of the fruiting season. Both will be influenced by sampling intensity. The first and last recorded dates are more strongly affected by outliers and sampling intensity, which makes it suitable only for highly systematic, intensive field surveys, or datasets which have been shown to be unbiased by sampling intensities. The influence of number of records on percentiles are non-linear, the percentile stabilises with increasing number of records, hence with few records and huge differences in records between years care must be taken (Kauserud et al., 2012). (4) Differences in vegetation and resource type between different regions, which can influence geographical-specific timing (Kauserud et al., 2008, 2010). The geographical structure is sometimes of interest in itself for describing how climate influences spatial distribution of fungal species (Wollan et al., 2008; Kauserud et al., 2011), and at an even broader scale for comparing trends between countries (Kauserud et al., 2012). (5) Different studies use different correction factors, which can influence interpretation. (6) Processes of lags (Kauserud et al., 2008, 2011) or autocorrelations (Kauserud et al., 2012) also need to be considered. In particular, if long-term changes are investigated some structure may appear in the residuals that potentially violates statistical assumptions. However, studying phenological changes over time within the data must

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always be the main aim, and correlative patterns of the covariance should be informative rather than an obstacle for testing. (7) Most of the statistical analyses of phenology performed so far have studied some parameter of the distribution of annual records (Gange et al., 2007; Kauserud et al., 2012), whereas alternative approaches could investigate the entire distribution of phenological records through Bayesian approaches (Sato et al., 2012; Diez et al., 2013). (8) Taxonomic or phylogenetic constraints, i.e. having an unbalanced taxonomic balance, may bias the results in one direction, e.g. if one genus is far more numerous than other genera. (9) Similarly, if datasets vary in their species composition, differences may become apparent if one particular 'guild' (e.g. saprotrophs or mycorrhizal species) of fungi is under or over represented in one set, compared with another. Thus, in addition to differences between taxa in terms of when they appear, there may also be differences in how phenological changes alter with time. To overcome such concerns, a structured covariance can identify random contributions of average/intercept as well as temporal change, both related to the genera as well as the species within genera (Kauserud et al., 2012). This will provide valuable information about the individuality of genera and species within genera with respect to average timing during a year as well as changes in the timing across years.

In the following section on changes in phenology we describe the emerging picture of changes in early year and autumn fruiting in northern Europe, differences amongst species and ecological groups, geographical differences, and the relationship between fruiting and climate. We have illustrated the main points with appropriate examples from the available literature. A rigorous mathematical comparison between the different published studies is beyond the scope of this article, for many of the reasons alluded to above.

Changes in fungal fruiting phenology

Many studies have recently revealed changes in the phenology of Earth's biota related to climate change (e.g. Fitter and Fitter, 2002; Peňuelas et al., 2002; Root et al., 2003; Both et al., 2004; Gordo and Sanz, 2005; Jonzén et al., 2006; Menzel et al., 2006). Most of these concern vernal changes in vertebrates, insects and plants, but fungal fruiting has also been dramatically affected (Table 1). The majority of fungal analyses have concerned northern Europe, though two studies from Asia have now been published (Yang et al., 2012; Sato et al., 2012), and one from North America (Diez et al., 2013). In northern Europe, fungal fruiting patterns have altered both in autumn and spring, and vary between species, ecological groups and bio-geographic zones. Elsewhere seasons are different but again patterns have altered. Here we concentrate on northern Europe where most reliable information from independent studies allows relatively straightforward comparison.

Changes in early year and autumn fruiting in northern Europe

Europe's climate is changing (Supplementary material 2) and so is its fungal phenology. In temperate and boreal ecosystems, the majority of macrofungi that produce ephemeral, fleshy fruit bodies do so in the autumn, though a few species typically fruit in spring and early summer, especially morels and other cup fungi (Pezizales, Ascomycota), and *Calocybe gambosa*. These spring fruiting fungi are fruiting progressively earlier in the UK and Norway – on average 18 d earlier now than in 1960 (Mattock et al., 2007; Kauserud et al., 2010). In both countries, early fruiting was correlated with high winter temperatures in Jan. and Feb.. Climatic conditions in 1 yr were also correlated with timing of fruiting the following year, perhaps explained by the need for mycelia to accumulate sufficient carbon, energy and nutrients before fruiting can occur.

Meanwhile, in the UK, in an analysis of 262 species of autumnal fruiters, 20 % of species have begun to fruit twice a year (in spring and autumn) since the mid 1970s (Gange et al., 2007; Mohammad, 2013; Supplementary material 3). However, differences exist among fungal guilds: while only 2.5 % of mycorrhizal species are showing bi-annual fruiting, this figure rises to 37 % in wood decay fungi. Furthermore, fungi considered to be vernal species, such as *Morchella esculenta* and *Morchella elata*, seem no longer to be so, with recent records now occurring later in the year, into autumn (Wearn et al., 2010).

The autumn fruiting season in Austria, Norway, the UK and Switzerland has widened considerably during the last 30 yr (Gange et al., 2007; Kauserud et al., 2012: Figs 1 and 2), and mean annual date of fruiting tends to be later (Kauserud et al., 2012). In southern England, the first autumn fruiting date averaged across all species has become significantly earlier, while the mean last fruiting date has become significantly later (Gange et al., 2007; Fig 1). This has resulted in a dramatic increase in the overall fruiting period, extending from 33.2 ± 1.6 d in the 1950s (Gange et al., 2007) to more than twice (69.1 ± 6.8 d) that by 2009. This extension of the northern European fruiting season parallels an extended vegetation growth season (Menzel et al., 2006). However, though the length of the fruiting season tends to increase on average, there is considerable variation between ecological groups, species, countries and studies, depending on the types of dataset used. These issues are considered separately below.

Differences amongst species and ecological groups

Species behave differently, some starting to fruit earlier, others starting to fruit later, some having a later end of fruiting,

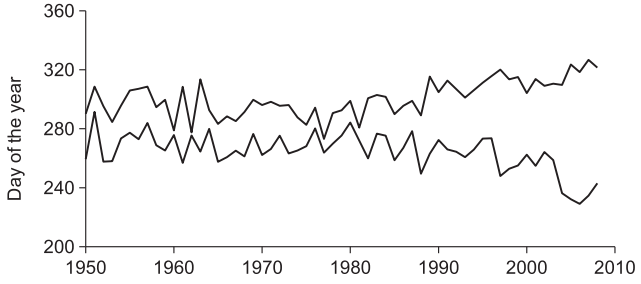

Fig 1 – The recent extension of the fungal fruiting season in southern England. Mean first fruiting date (lower line) and mean last fruiting date (upper line) for 386 fungal species over 59 yr. The mean length of the fruiting season in the 1950's was 28.2 d and in the 2000's 69.1 d. Updated from Gange et al. (2007).

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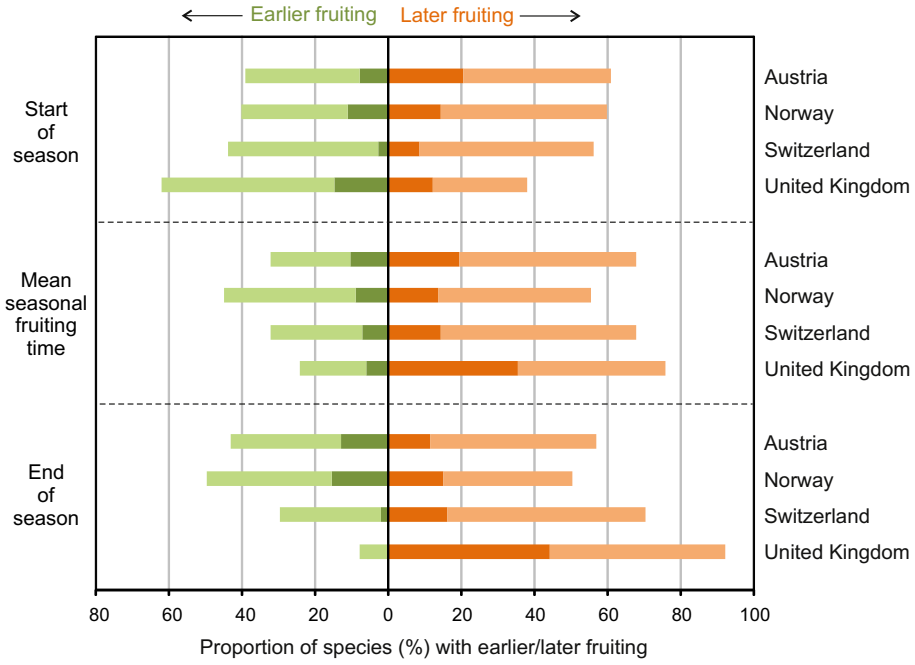

Fig 2 – Proportion of species whose start, mean and end of the fruiting season has changed during 1970–2007, in Austria, Norway, Switzerland and the UK. The start of the season was indicated by the 2.5th percentile and the end by the 97.5th percentile, rather than the actual first and last observations. The linear temporal trends were estimated by a generalised least square procedure, assuming autoregressive process and prior adjustment for both geography and sampling intensity. Bars are the proportion of all species with earlier (left bars) or later (right bars) fruiting; the dark bars indicate significant species. Plotted from the data (746 297 records of 486 species) used in Kauserud et al. (2012).

others having an earlier end of fruiting, and others remain unchanged. There are, thus, different ways by which the length of the fruiting season can alter (Table 3). For example, in southern England, 25% of species have started to fruit earlier (with an advancement of over 8 d decade^{-1}), while 40% now start to fruit later (over 7 d decade^{-1}) (Gange et al., 2007). While this has usually led to an extended fruiting season, for a few species the fruiting season has contracted (Fig 2). Again, there are differences between fungal groups. While 33% of wood decay species have a significantly extended fruiting season, only 10% of mycorrhizal species have done so. Meanwhile, the fruiting season of 10% of mycorrhizal species has significantly contracted in length, but not any litter saprotrophs (i.e. those species that occur in the same habitat, but are not mycorrhizal) have done so (Fig 3). There are also differences amongst species and ecological groups over the whole of the UK, not just the south, and in Austria, Norway and Switzerland (Kauserud et al., 2012), though because different types of dataset were used, and the datasets contain different species, comparison between datasets is difficult (Kauserud et al., 2013). This fact notwithstanding, in Austria, Norway, the UK and Switzerland, ectomycorrhizal fungi tend to have a more compressed fruiting season than saprotrophs, again probably partly reflecting the fact that the former can receive fruiting cues from their hosts, e.g. changes in carbohydrate allocation (Kauserud et al., 2012); both probably also receive microclimatic fruiting cues and nutrition is also likely to be important. While these overall trends are clear between ecological groups, there are differences within groups and even within genera having the same general ecological role (Fig 4). In the genus *Russula*, for example, some species have shown an extension of their fruiting season, while others have shown a contraction (Fig 4). These temporal changes suggest that fungi, like many other organisms, show individualistic responses to changes in climate (Stewart, 2009).

Further evidence for individualistic effects is seen if the responses of species that fruit early or late in the season are considered. The regression coefficient of fruiting date against year indicates the rate of change of the timing of the first, last

Table 3 – Change in length of fruiting season in Southern England resulting from changes in first and last fruiting date according to ecological group. Note that changes are typical of a particular ecological group though species within a group and even a genus do vary (see Fig 4). Extracted from Mohammad (2013)

	First fruiting date	Last fruiting date	Fruiting season
Woodland litter saprotrophs	Unchanged	Later	Large extension
Deciduous mycorrhizas	Later	Later	Small extension
Coniferous mycorrhizas	Earlier	Earlier	Unchanged
Wood decayers	Earlier	Unchanged	Large extension

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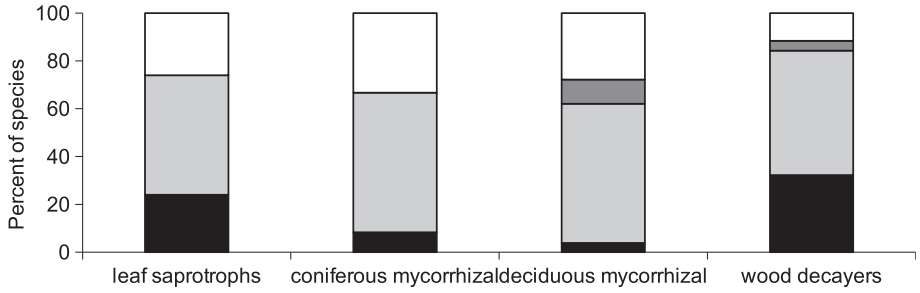

Fig 3 – The proportion of species in different fungal guilds, showing an extension or contraction in their fruiting seasons. Data are from southern England (see Supplementary material 1) and cover the 59 yr from 1950 to 2009. Black segments of bars, significant extension in the season length; pale grey segments, extension, but not statistically significant; dark grey segments, significant contraction in season length; white segments, contraction, but not statistically significant.

and mean fruiting days. Plotting the regression coefficient of change in mean fruiting date for each species against the overall mean date of occurrence of each species across all years also reveals clear trends among ecological groups (Mohammad, 2013). For saprotrophs in deciduous and coniferous litter, and dead wood, earlier fruiting species have large positive coefficients, indicating trends to later fruiting. In contrast, later fruiters have negative coefficients, indicating trends to earlier fruiting. This may reflect the different responses of early and late fruiters to temperature and rainfall (see below).

Though mycorrhizal fungi and many saprotrophs continue fruiting later in the year, the fruiting season of mycorrhizal species is often more compressed than that of saprotrophs, though no differences were seen at La Chaneaz, Switzerland (Büntgen et al., 2013). This difference is probably at least partly due to fruiting responses of mycorrhizal species depending on fruiting cues from their hosts as well as cues from the climatic environment. In the UK, there was a distinct difference between fruiting of coniferous and deciduous mycorrhizal species, the former remaining on average largely unchanged, the latter tending to start and end fruiting later (Gange et al., 2007). This effect relates to the host and is not simply due to different hosts being associated with different fungal species. This was shown by comparing fruiting times of those fungal species that are mycorrhizal with both conifers and deciduous trees: these fungi (e.g. *Amanita citrina*, *Laccaria laccata* and *Russula ochroleuca*) had delayed fruiting when associated with deciduous trees, whereas when they were associated with conifers their fruiting was delayed less, not at all, or even advanced.

Geographical differences in timing of fruiting

Not surprisingly time of fruiting depends on geographical location. There is a distinct north–south trend from southern UK to northern Norway, the mean fruiting date for spring fungi in northern Norway being about 120 d later than in southern UK (Kauserud et al., 2010; Fig 5). Similar latitudinal patterns have been seen in plant phenology (Ovaska et al., 2005). The rate of change in plant phenology varies across Europe, depending on regional differences in extent of climate change (Menzel et al., 2006). Likewise, changes in fungal phenology vary between regions. For example, while in the UK many species now have an earlier start to the autumn fruiting season (as described above), in Austria, Norway and Switzerland most species now

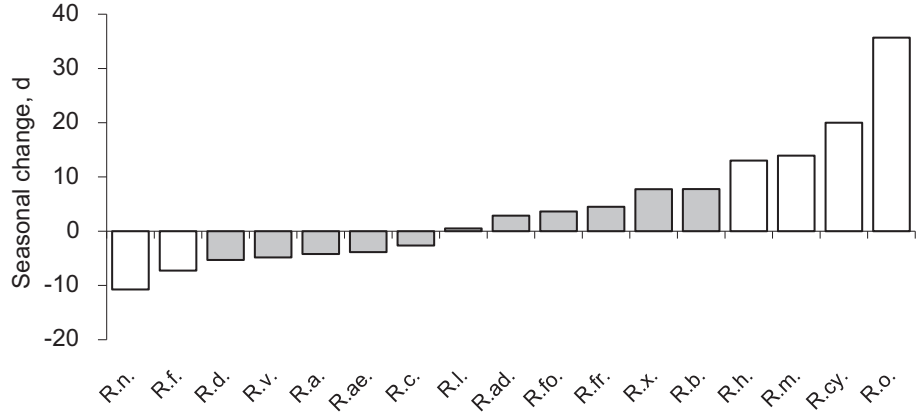

Fig 4 – Changes, between 1950 and 2009, in the length of the fruiting season in the ectomycorrhizal genus *Russula* in southern England (see Supplementary material 1). White bars indicate species showing a statistically significant change. Key to species: R.n., *R. nigricans*; R.f., *R. fellea*; R.d., *R. delica*; R.v., *R. virescens*; R.a., *R. atropurpurea*; R.ae., *R. aeruginea*; R.c., *R. claroflava*; R.l., *R. lepida*; R.ad., *R. adusta*; R.fo., *R. foetens*; R.fr., *R. fragilis*; R.x., *R. xerampelina*; R.b., *R. betularum*; R.h., *R. heterophylla*; R.m., *R. mairei*; R.cy., *R. cyanoxantha*; R.o., *R. ochroleuca*.

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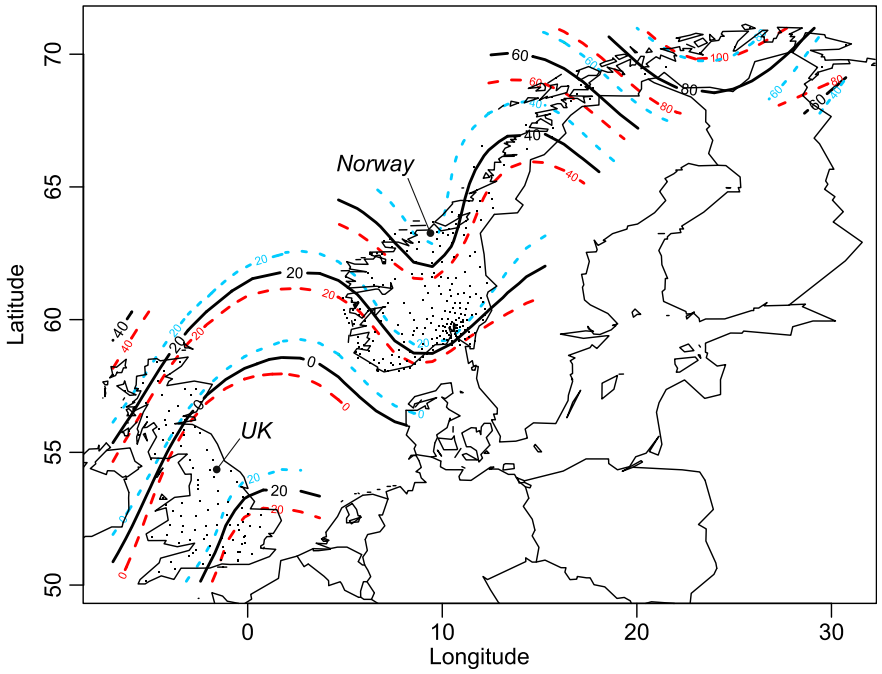

Fig 5 – Difference in the time of early year fruiting in Norway and the UK. Isopleths indicating the mean number of days difference in fruiting compared with the 0 isopleth. The 0 isopleth is the mean fruiting data for the combined UK and Norway datasets. Dashed isopleths are the 95 % confidence interval. Redrawn from Kauserud et al. (2010).

start to fruit later (Kauserud et al., 2012; Fig 2). Though the end of the fruiting season is getting later in all of these countries, the rate of change varies ranging, for saprotrophs, from 1.1 d later per decade (Austria) to 6.4 d later (UK). The oceanic climate of the UK, with mild winters and cool summers, is probably the main reason for the differences in phenological changes between these four countries.

Relationship between fruiting and climate

A wide range of environmental factors influence the timing and development of fruit bodies, including nutritional factors, gaseous regime, pH, light, microclimate, disturbance, and inter- and intra-specific mycelial interaction (Moore et al., 2008). The rate of supply and ease of use of substrates are major determinants of fruit body formation, and it is, therefore, not surprising that wood decay basidiomycetes fruit less readily than litter decayers which in turn fruit less readily than dung fungi. Similarly, early colonising r-selected macrofungi fruit more readily than later-colonising K-selected fungi (Cooke and Rayner, 1984; Rayner and Boddy, 1988). Light has a wide range of effects on basidiomycete fruiting, determining whether or not fruit bodies are produced, their development and numbers produced (Moore et al., 2008). Many ascomycete species require exposure to light before they will fruit (Elliott, 1994). *In vitro* studies have shown that optimum temperatures for fruiting cover a narrower range than for mycelial growth (Moore et al., 2008). For example, a downshift of 5–10 °C is often needed to induce fruiting in cultivated basidiomycetes (Stamets, 1993). The downshift can sometimes be for a short duration. The 'winter fungus' *Flamulina velutipes* fruits in late autumn to spring in nature; it will fruit at a continuous 20 °C or following 12 hr depression at 15 °C (Kinugawa and Furukawa, 1965). In the cultivated mushroom *Agaricus bisporus*, though fruit body initials are produced at 24 °C, a downshift to 16 °C is required for further development (Flegg, 1978a,b).

Soil moisture availability is a major determinant of fruiting. If the water potential is too low, fungi are unable to obtain sufficient water for fruit body development (Barroetavena et al., 2008). In contrast to saprotrophs, mycorrhizal fungi can receive water from the host tree through hydraulic lift (nocturnal water transfer from the tree to the associated mycorrhizal symbiont) (Querejeta et al., 2003), and transfer this water to the sporocarps (Lilleskov et al., 2009). If water content is too high aeration is reduced, which can also be inhibitory. Elevated CO_2 can suppress basidiome production and alter morphology (Moore et al., 2008). Relatively high humidity is often conducive to fruit body initiation (Stamets, 1993), though if it is too high development can fail.

In summary, climatic variables are important in initiating fruiting and development of sporocarps, though other environmental factors can also affect fruiting. Fruiting, however, ultimately depends on sufficient nutrients, and acquirement of nutrients in turn is affected by climate. All of this is superimposed on the life-history strategy of a species, not least whether it is saprotrophic or mycorrhizal, the latter probably also experiencing cues from its host, which also depends on ambient climate conditions. It, therefore, comes as no surprise that fruiting patterns are changing as climate does, and that environmental moisture and temperature regimes often explain a lot of the variation in timing of fruit body production (see below and references herein).

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The effects of climatic variables, e.g. temperature, precipitation and solar radiation, on fruiting in the natural environment are almost always interrelated, associated not only with prevailing conditions and conditions in the recent past, but also being affected by conditions in the previous year, so-called lag effects. For example, elevated Jul. temperature and Aug. rainfall resulted in earlier fruiting on average of spring fruiting species in Norway and the UK, whereas elevated Oct. temperature was correlated with delayed fruiting the following spring (Kauserud et al., 2010). Different studies have shown different effects, presumably relating to differences between ecological groups, ecosystems and types of data available. No clear pattern emerges, so we just present examples for saprotrophs here. In southern UK, over 90 % of all saprotrophs that normally fruit early in the autumn season (in Sep.) showed a significant relationship between average fruiting date and late summer temperature and rainfall (Moore et al., 2008). In years when Jul. and Aug. temperatures were high and rainfall low, fruiting was delayed, concurring with other single-season studies (Salerni et al., 2002). An analysis of local meteorological data showed that both Jul. and Aug. mean temperatures have increased significantly over the last 30 yr, while rainfall has decreased, but less markedly (see also Supplementary material 2). In contrast, for 88 % of species normally fruiting in Oct. and Nov., fruiting was earlier in years when Aug. temperatures and Oct. rainfall (which have increased over time) were high. In the Swiss fungus reserve La Chanéaz forest, during 1975–1999, appearance of fruit bodies was correlated with Jul.–Aug. temperatures, a 1 °C increase resulting in a 7 d delay (Straatsma et al., 2001). With regard to spring fruiting, higher winter temperatures result in earlier fruiting in Norway and the UK; in Norway every 1 °C increase in Jan. resulted in 1 d earlier fruiting, whereas in the UK a 1 °C rise in Jan. and Feb. corresponded to fruiting 3 d earlier (Kauserud et al., 2010). Elevated temperatures will allow increased mycelial activity; hence resources for fruiting are acquired earlier. The latitudinal patterns described above also relate in part to climatic effects.

Changes in fruit body yields

Factors affecting production of basidiomycete fruit bodies have only been examined in detail for a few species, especially those cultivated commercially (e.g. Kues and Liu, 2000) and a few others that fruit readily in artificial culture (Moore et al., 2008). In the field, it is clear that fruit body production varies dramatically from year to year, and that the amount, duration and frequency of fruiting are influenced by numerous environmental factors – both biotic and abiotic, as well as complex interactions among them. Although *in vitro* culturing experiments are able to reveal causal relationships between various treatment effects and fruit body yields, they are limited by the few combinations of variables that can be studied, and are biased towards the species that are selected – confined largely to those that fruit prolifically and soon after colonisation. Only observational field surveys can provide information about the multitude of factors involved in real world conditions, including both r- and K-selected species. Several short and long-term field surveys have related fruit body yields recorded as weight to environmental factors, including climate variation, especially rainfall and ambient temperature (Table 4).

Table 4 – Long-term dataset analyses of climate change effects on basidiocarp yields

Location	Period	Type of data	Factors correlated with high yield	References
Yunnan, China	2000–2010	Counts of *Tricholoma matsutake* (4 578)	Positive correlation: high temperature and high precipitation in Aug. Negative correlation: high temperature in Jun; and high humidity in Nov/Dec (the preceding year) to May.	Yang et al. (2012)
Yukon, Alaska	1993–2007	Counts and biomass of epigeous basidiocarps (8 650)	Positive correlation: Jun. rainfall (current year) and previous year May rainfall.	Krebs et al. (2008)
Catalonia, Spain	1997–2001	Weights of epigeous basidiocarps (16 103) (ECM + some saprotrophs)	Positive correlation: mean annual precipitation; and precipitation minus Sep./Oct. evapotranspiration plus minimum Aug. soil temperature.	Martínez de Aragón et al. (2007)
France, Italy, Spain	1970–2006	Truffle (*Tuber melanosporum*) harvest data	Positive correlation: summer precipitation. Negative correlation: summer temperature.	Büntgen et al. (2012a)
La Chanéaz, Switzerland	1975–2006	Counts of epigeous ECM basidiocarps (65 631)	Positive correlation: summer precipitation. Positive correlation: Aug. maximum temperature and weighted week of appearance.	Büntgen et al. (2012b))
La Chanéaz, Switzerland	1975–1999[a]	Counts of epigeous basidiocarps (71 222)	Positive: correlation: precipitation in Jun.–Oct.	Straatsma et al. (2001)
La Chanéaz, Switzerland	1977–2006	Counts of epigeous basidiocarps	Positive correlation: tree growth (tree ring width).	Egli et al. (2010)
Northern Ireland	1974–1987	Counts of epigeous fruit bodies	Positive correlation: temperature 2–4 months prior to recording dates over a 10-yr-period; precipitation in the prior 5 months except if immediately before fruiting.	Eveling et al. (1990)

[a] Excluding 1980–1983.

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Summer precipitation is often positively correlated with high autumn yield (Table 4), though in Northern Ireland yield was lower if rain came immediately prior to fruiting (Eveling et al., 1990). In dry ecosystems (with precipitation less than 650 mm yr^{-1}), rainfall of the current year is the driving factor for mushroom growth, e.g. in the Pyrenees (Bonet et al., 2010), Argentina (Barroetavena et al., 2008) and Catalonia (Ogaya and Peñuelas, 2005).

Several studies showed a lag in response to rainfall and other climatic conditions in the preceding year(s) (Krebs et al., 2008; Egli et al., 2010; Yang et al., 2012), reflecting the acquisition of energy and nutrients for fruiting, by perennial mycelia over an extended period. Moreover, high yields 1 yr are often followed by low yields the following year (Krebs et al., 2008), presumably due to insufficient time to build up resources to allocate again to fruiting. It is not just precipitation that is critical to fruit body production, but also evapotranspiration (Martínez de Aragón et al., 2007), implying the importance of soil water availability, particularly in arid environments such as in most of the Mediterranean Basin (Büntgen et al., 2012). Studies employing experimental irrigation (Wiklund et al., 1995) and drought (Ogaya and Peñuelas, 2005) support these field observations.

The effect of temperature on yields seems to vary more. For example, negative (Büntgen et al., 2012), positive (Eveling et al., 1990) and non-effect (Krebs et al., 2008) of high summer temperatures have been observed. Hence, the effect of temperature could be more ecosystem and site dependent. In drier areas with a high level of evapotranspiration, high temperatures may have a deleterious effect on the metabolic activity of the mycelia. However, high temperatures could also lead to high yields through a stress or escape response (Yang et al., 2012).

The nutritional mode is also of importance. While saprotrophic fungi probably are more directly influenced by climatic factors, ectomycorrhizal fungi are also dependent on interactions with their host and the host's photosynthetic activity, and hence on how the host is affected by climate. However, at La Chanéaz reserve in Switzerland, there was no evidence of differences in productivity of ECM fungi relative to saprotrophs associated with climatic variability (Straatsma et al., 2001; Büntgen et al., 2013).

There is some evidence of temporal changes in productivity. At La Chanéaz fungus reserve Switzerland, there has been a dramatic increase in number of fruit bodies since 1990 (Büntgen et al., 2011). It was speculated that this yield increase was due to improved growth conditions caused by climate change, for both the ECM fungi and the host plants. This was supported by a positive correlation between fruit body numbers and tree ring width, suggesting a close link between host plant growth and fruit body production of the associated ECM fungi (Egli et al., 2010). In contrast, there is evidence for a long-term decline in yields of the Périgord black truffle *Tuber melanosporum* in France, Italy and Spain (Büntgen et al., 2012). High yields of *T. melanosporum* correlate with high summer rainfall (especially in France and Spain), whereas low yields are correlated with high summer temperatures, corresponding to reduced soil moisture availability. Since climate models predict a further increase in temperature and decrease in precipitation for most of the Mediterranean Basin, leading to higher evapotranspiration and lower soil water content, further decrease in truffle yields is expected for this region (Büntgen et al., 2012).

In most analyses of factors affecting fruit body productivity based on field survey data, the effect of individual components have been modelled but interactions between different factors may be most important, for example between rainfall and temperature, and over different time spans. However, such complex interaction effects are difficult to study and require large long-term datasets. Moreover, many relevant factors have been ignored including physical edaphic factors. A major question that we cannot yet answer is: how will climate change affect fruit body yields? The answer will almost certainly not be simple, and is likely to be context-dependent.

Range shifts

Mycelial growth, survival, physiology and competitive ability all respond sharply to alterations – often even small ones – in temperature and water potential *in vitro*. Hence, it is expected that an increase in global temperatures and changes in rainfall distribution (see Supplementary material 2) may lead to significant changes in fungal species distribution patterns. Numerous fungi, and especially animal and plant pathogens have, during the last few years, gone through dramatic range changes (Fisher et al., 2012; Santini et al., 2013; Bebber et al., 2013), and for some species it has been speculated that climate change may have a role, e.g. with the emergence of the skin-infecting amphibian chytrid, *Batrachochytrium dendrobatidis* (e.g. Pounds et al., 2006) though this is debated (Rohr et al., 2008). Likewise, it has been speculated that the rapid expansion of forest pathogens like *Hymenoscyphus pseudoalbidus* (=*Chalara fraxinea*), causing ash dieback, is enhanced by climate change (Santini et al., 2013). In the Northern Hemisphere, fungal pests of crops have been increasingly detected towards the north, since 1960 (Bebber et al., 2013).

The distribution ranges of many fungi support temperature as being a major determinant of the observed spatial patterns. Numerous fungi have wide distributions longitudinally, e.g. circumpolar arctic or boreal taxa (Carlsen et al., 2011; Seierstad et al., 2013) but much less so latitudinally. In a study from Norway, where fungal distribution patterns were related to 75 environmental predictor variables (Wollan et al., 2008), a close link between temperature and species distributions was found. For most of the nine species analysed, temperature during the early growing season (May–Jul.) appeared to be the most important for the species distributions, with autumn temperatures less critical. This could be because during spring and early summer new mycelia may establish and expand.

The molecular and genetic basis that determines a fungus' distribution has been little studied. However, by use of molecular data, Ellison et al. (2011) linked the divergence of two sub-populations of *Neurospora crassa* to adaptations to different temperature regimes. The northernmost population had a higher fitness at low temperature (10 °C), and several of the differentiated genes had functions related to the response to cold temperatures. Interestingly, another of the genes that was differentiated between the populations was the circadian

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oscillator gene '*frequency*' (*frq*), which is involved in coordinating the day–night cycle. This suggests that the 2.4–10.6° difference in latitude with associated day length differences may be another important environmental parameter. Photoperiod has certainly been noted as a key limiting factor for climate-induced phenological shifts in plants (Körner and Basler, 2010).

There are numerous problems when studying changes in the distribution of fungi. Most fungal species have been defined based on fruit body morphology, but often it is unclear whether a morphospecies represents one or several biological species with different distributions (e.g. Carlsen et al., 2011; Seierstad et al., 2013). Moreover, for most fungal morphospecies extant distributional ranges are largely unknown, especially outside Europe and parts of North America – the regions where most mycologists have worked. Many taxa may have far wider distributions than can easily be recorded by registering ephemeral fruit bodies. Furthermore, many fungi produce inconspicuous fruiting structures which make them difficult to record even by experts. There is also a large diversity of fungi that do not produce visible structures at all (e.g. Rosling et al., 2011). Even though great progress has recently been made in high throughput DNA sequencing of fungal diversity (Lindahl et al., 2013), we still rely mainly on fruit body records for estimating species distributions. Distribution (niche) model approaches (Wollan et al., 2008), such as MaxEnt (Phillips et al., 2006), are useful ways to learn more about fungal distribution patterns. From relatively few records the tentative ranges of species can be modelled and verified by independent field observations.

Changes in host affinity

It is well-documented that many species have different hosts in different regions, and this is likely to at least partly depend on climate effects. Further, the outcome of interspecific mycelia interactions often varies depending on microclimate (Boddy, 2000), which itself may depend, at least partly on host. For example, the saprotrophic ascomycete *Daldinia concentrica* fruits on ash (*Fraxinus excelsior*) and occasionally in beech (*Fagus sylvatica*) in the southern UK, and on birch (*Betula* spp.) in the north (Parfitt et al., 2010). It is latently present in functional sapwood, not developing overtly as mycelium until sapwood begins to dry. Rates of drying, temperature and gaseous regime all affect which species of latent fungi develop overtly in standing trees (Hendry et al., 2002). Difference in climate in the south and north of the UK is probably the main reason for this fungus developing on different host species.

When introduced into new habitats, some fungi have shifted their host range, compared with their area of origin (e.g. *Amanita phalloides*; Wolfe and Pringle, 2012). However, evidence for a change in host of fungi due to climate change is considerably rarer. *Auricularia auricula-judae* in the UK may provide an example. The host range of *A. auricula-judae* appears to have expanded in southern UK since the late 1970s, and it now fruits earlier and for longer (Gange et al., 2011). In the 28 yr before 1978, *A. auricula-judae* was found only on elder (*Sambucus nigra*) in surveys within a 30 mile radius of the city of Salisbury, but now has been reported on 16 hosts, fruiting each year on up to six host tree species, after elder the most common host now being beech (*F. sylvatica*). This expansion of host range coincides with the change in phenology of fruiting. Further, since the 1990s, the number of fungal species fruiting on *S. nigra* increased from three pre-1990 to 12 in 2007. It is possible that such host shifts result from changes in foraying quality over time (Heilmann-Clausen and Læssøe, 2012; Gange et al., 2012). However, if this were true, then one would expect to see similar artefactual shifts in many other species too and similarities between fungal guilds. In a recent analysis of records from southern England, this was not so (Mohammad, 2013). In that study, 84 % of litter saprotrophic species appeared to have expanded their host association over the last 59 yr, while significantly fewer (53 %) mycorrhizal species have done so.

Conclusion and future direction

The above examples clearly emphasise that we have only taken the very first steps towards elucidating the effects of climate change on fungal fruiting patterns and distributions. However, one emerging pattern is that climate change is affecting fruiting in many regions, though there is considerable variation in how specific fungi respond and, moreover, that responses may differ in different areas (Kauserud et al., 2012). Furthermore, several studies indicate highly complex relationship between fruiting patterns and environmental variables, such as temperature and water availability in soil and air. Unravelling these relationships requires extensive and high quality datasets. One limiting factor is the availability of only a few long-term monitoring datasets from anywhere in the world, where the appearance of fruit bodies has been surveyed in a rigorous way (but see Gange et al., 2007; Martínez de Aragón et al., 2007; Büntgen et al., 2011). Hence, there is an urgent need for establishing additional time series, and which also include more detailed data on edaphic factors and aboveground climate. In addition to fruit body records, new surveys should include soil samples for DNA and/or RNA based analyses of fungal communities (see Lindahl et al., 2013). Most studies conducted so far have looked at correlations between environmental conditions and fruiting patterns in the field. Nonetheless, the following conclusions can be made for Europe: (1) On average, the fruiting season of the majority of species has extended, though for some species it has contracted. The consequence is that (2) the mean annual day of fruiting in Austria, Norway, Switzerland and the UK has become later. (3) Different species and ecological groups behave differently. For example, though on average both saprotrophic and mycorrhizal fungi now continue to fruit later in the year, mycorrhizal species tend to have a more compressed season than saprotrophs. (4) Time of fruiting depends on geographical location. (5) Some fungi now fruit early in the year as well as in autumn, and the fruiting of vernal species is getting earlier. (6) Fruit body yields vary dramatically from year to year, and the amount, duration and frequency of fruiting are influenced by numerous environmental factors. (7) There is evidence of fungal shifts to different hosts, probably at least partly associated with changing climate. Globally,

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ranges of species are likely to shift with changing climate, but little information is currently available.

Obviously, it is impossible to analyse the complexity of the real world under laboratory conditions but a next step should also be to assess experimentally causative relationships. This should not just involve those fungi that fruit readily in culture – which tend to be species with r-selected characters – but those which are relatively more K-selected fruiting later in their life cycles, intermittently and/or are associated with hosts that provide cues for fruiting. Fungi are also an important food source for many invertebrates (Boddy and Jones, 2008) and some vertebrates. Although we have some understanding of the effects of grazing on mycelium and *vice versa* (Crowther et al., 2012), and of the invertebrate species that live and breed in fruit bodies (Stokland et al., 2012), we have little knowledge of multi-trophic effects induced by changes in the distribution and activity of fungal mycelium or fruit bodies (but see A'Bear et al., 2013). This calls for both rigorous observational field studies and experiments.

For the analyses of climate-induced shifts in fungal distributional ranges valuable data are continuously being added to public databases such as GBIF (www.gbif.org), and will provide data sources for future analysis. Distribution modelling analyses based on digitised fungal records (Wollan et al., 2008; Bebber et al., 2013) have a great potential for elucidating historic shifts in fungal ranges as well as forecasting future range shifts under various climate change scenarios.

The availability of new DNA technologies opens up many new research pathways. Based on genome sequence analyses it is now possible to establish links between the responses of fungi to climate, and of their genomic features and gene content (see Ellison et al., 2011). The analysis of climate change-induced changes in the transcriptome/secretome of an organism will also add new insight to the field. Performing evolution experiments to investigate evolutionary changes (e.g. Dettman et al., 2007) induced by climate change would be well worthwhile.

The most important areas for future endeavour, include long-term monitoring, interdisciplinary collaboration, open data policy, combining field observation and laboratory experimentation, and linking evidence from various spatio-temporal scales.

Acknowledgements

We thank the Research Council of Norway for their financial support to the project 225041/E10, and anonymous reviewers of the manuscript for suggested improvements. AM would like to thank the Malaysian Ministry of Higher Education for funding and ACG thanks his father and the many volunteers who helped to collect records of fungal fruiting in southern England.

Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.funeco.2013.10.006

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Please cite this article in press as: Boddy L, et al., Climate variation effects on fungal fruiting, Fungal Ecology (2013), http://dx.doi.org/10.1016/j.funeco.2013.10.006

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Please cite this article in press as: Boddy L, et al., Climate variation effects on fungal fruiting, Fungal Ecology (2013), http://dx.doi.org/10.1016/j.funeco.2013.10.006