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Climate variation effects on fungal fruiting

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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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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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