

Rapid and recent changes in fungal fruiting patterns

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Many studies have demonstrated recent phenological responses to climate change, but these largely involve higher organisms, such as plants, insects or birds, restricted to events in spring (1). Autumnal events have received far less attention, even though the end of the growing season has seen significant delays (2). Fungi provide vital ecosystem services through decomposition, nutrient cycling and soil aggregation, yet they are missing from previous considerations of ecosystem responses to global change (3). In this study, we analysed a data set consisting of over 52,000 individual fungal fruiting records, from nearly 1,400 localities, collected in southern England over the period 1950-2005. We extracted information on a total of 315 autumnal fruiting species, each of which had been recorded in more than 20 y (4).

The first fruiting date averaged across all species has become significantly earlier, while average last fruiting date has become significantly later (Fig. 1A). The increase in the overall fruiting period is dramatic; in the 1950s it was 33.2 ± 1.6 d, but this has more than doubled to 74.8 ± 7.6 d in the current decade. For the species that show significantly earlier first fruiting dates ($n = 85$), the average advancement is 8.6 ± 0.6 d decade⁻¹, while for species showing significantly later last fruiting dates ($n = 105$), the delay is 7.5 ± 0.5 d decade⁻¹, both of which are greater than equivalent spring data previously reported for higher organisms (5).

The alteration in fungal fruiting mirrors changes in British temperatures that have occurred since 1975 (6). To substantiate this, we examined relations between fruiting dates of each species and monthly records of local temperature and rainfall (4). Over the 56 y, August temperatures have increased ($F_{1,54} = 11.4$, $P < 0.01$), as has October rainfall ($F_{1,54} = 5.8$, $P < 0.05$). The increase in late summer temperatures and autumnal rains has caused

early season species to fruit earlier and late season species to continue fruiting later. Seventy eight (91%) of the species showing an advanced fruiting date have a significant relation between first fruiting date and August temperature, while 92 (88%) of the species showing later last dates could be explained by positive relations between August temperature and October rainfall.

We noticed that 47 (59%) of the deciduous mycorrhizal species showed a delay in last fruiting date, while no coniferous mycorrhizal species were delayed. To examine this further, we studied the 11 mycorrhizal species that were recorded beneath both coniferous and deciduous hosts. Average fruiting date in each year was calculated and regressed against time (56 y). Eight of the species showed a significantly larger regression coefficient when growing beneath deciduous hosts (Fig. 1B). Therefore, the fruiting season of these species has changed in a habitat-dependent manner. If these responses were due to microclimatic differences beneath deciduous and coniferous trees, then there would likely be similar differences in fruiting patterns of non-mycorrhizal forest floor fungi. To examine this possibility, we compared regression coefficients of seven non-mycorrhizal leaf litter decay species and a further seven wood decay fungi that occurred in both forest types. In no case did the regression coefficient differ (all $P > 0.05$), thus microclimatic effects can be discounted. These data suggest that changes in the temporal allocation of nutrients to roots have occurred in deciduous forests, but not in coniferous woods, where there is no single large loss of leaf material. Nutrients are intercepted by the mycorrhizal species and used for fruit body production (7).

Furthermore, climate warming seems to have caused significant numbers of species to begin fruiting in spring as well as autumn (Fig. S1). Given that active mycelial growth is

required before sporophore production, this is strong evidence that the mycelium of certain species must now be active in late winter and early spring as well as late summer and autumn, suggesting increases in decay rates in forests.

References and Notes

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8. We are extremely grateful to all those who collected fungi, especially Irene Gange, the late Jim Hindley, Ailsa McKee, Wendy Freemantle, Rosemary Nicholls and Ron Chapman.

Supporting Online material

www.sciencemag.org

Materials and methods

References

Fig. S1

Fig. 1. (A) Average first fruiting date (lower line) and average last fruiting date (upper line) of 315 fungal species over 56 years. The underlying pattern is represented by lowess (locally weighted scatter plot smoother) lines. **(B)** Regression coefficients for mean fruiting date v. years for 11 mycorrhizal fungal species when growing under coniferous or deciduous trees. Key to legend: A.C.: *Amanita citrina*, A.r.: *A. rubescens*, C.t.: *Cantherellus tubaeformis*, H.c.: *Hebeloma crustuliniforme*, L.a.: *Laccaria amethystina*, L.l.: *L. laccata*, P.i.: *Paxillus involutus*, R.a.: *Russula atropurpurea*, R.o.: *R. ochroleuca*, R.x.: *R. xerampelina*, T.t.: *Tricholoma terreum*. Asterisks above bars indicate a significant difference in coefficients between the host types at $P = 0.05$.