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 involved higher organisms, such as plants, insects, or birds, and were 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 analyzed a data set consisting of over 52,000 individual fungal fruiting records, from nearly 1400 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 years (*4*).

The first fruiting date averaged across all species has become significantly earlier, whereas average last fruiting date has become significantly later (Fig. 1A). The increase in the overall fruiting period is dramatic; in the 1950s, the average (±SE) was 33.2 ± 1.6 days, but this has more than doubled to 74.8 ± 7.6 days in the current decade. For the species that show significantly earlier first fruiting dates (n = 85), the average advancement is 8.6 ± 0.6 days decade^{-1}, whereas for species showing significantly later last fruiting dates (n = 105), the delay is 7.5 ± 0.5 days 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 past 56 years, 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, whereas 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, whereas 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 years). 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 nonmycorrhizal forest-floor fungi. To examine this possibility, we compared regression coefficients of seven nonmycorrhizal 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 be active in late winter and early spring as well as late summer and autumn, suggesting increases in decay rates in forests.

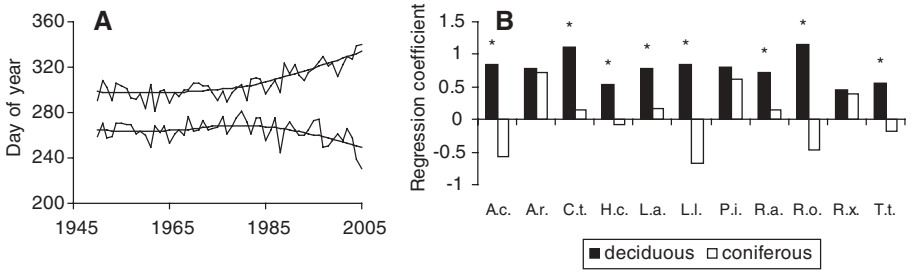

Fig. 1. (**A**) Average first fruiting date (lower line) and average last fruiting date (upper line) of 315 fungal species over 56 years. The underlying pattern is represented by lowess (locally weighted scatter plot smoother) lines. (**B**) Regression coefficients for mean fruiting date versus years for 11 mycorrhizal fungal species when growing under coniferous or deciduous trees. A.c. represents *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*; and T.t., *Tricholoma terreum*. Asterisks above bars indicate a significant difference in coefficients between the host types at P = 0.05.

References and Notes

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Supporting Online Material

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Materials and Methods
Fig. S1
References

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Supporting Online Material for

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Supporting Online Material

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Information on responses of higher organisms to climate change is dominated by events in spring. Far less is known about autumnal events and virtually nothing about communities of microorganisms. We analysed autumnal fruiting patterns of macrofungi over the last 56 years and found that average first fruiting date of 315 species is earlier, while last fruiting date is later. Fruiting of mycorrhizal species that associate with both deciduous and coniferous trees is delayed in deciduous, but not in coniferous forests. Many species are now fruiting twice a year, indicating increased mycelial activity and possibly greater decay rates in ecosystems.

Materials and methods

The data set consists of 52,382 records of sporophores gathered over a 56 y period. A total of 201 observers contributed records from 1,391 different localities, all within a 30 km radius of Salisbury, Wiltshire, UK. To avoid bias, localities were not searched on a systematic basis and each was selected at random on any date. Each locality was visited at least once per year and each searched for at least 3 h at a time. A sporophore was only recorded if it was freshly produced; perennial species with permanent sporophores were excluded from the analysis. EG collated all records and performed all identifications, with 'difficult' species confirmed by Royal Botanic Gardens, Kew. At least one collection was made in every week of every year and dates are accurate to the nearest 3 d. Collections occurred with equal frequency over the years, with no significant trend in the number of collections per year ($F_{1,53} = 2.3$, $P > 0.05$).

A total of 315 species were assigned to one of six habitat types: i) grassland saprotrophs (n = 44); ii) deciduous litter saprotrophs (n = 50); iii) coniferous litter saprotrophs (n = 9); iv) wood (e.g. twig, log or stump) decayers (n = 118); v) mycorrhizal with deciduous trees (n=82) and vi) mycorrhizal with coniferous trees (n = 12) (identified using *1*). The average date of first and last fruiting, (expressed as Julian day with adjustment for leap years) of all species was calculated for each year. The average fruiting date of each species in each year was calculated as the mean of all records for that species in each year. We used the conservative method of linear regression 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. Data from all habitat categories represent only Basidiomycota with the exception of wood decaying fungi, in which 20% were Ascomycota. We compared the regression coefficients of these two groups and found no significant difference ($F_{1,114} = 2.5$, $P > 0.05$) and so included both in the analysis.

The underlying pattern in mean first and last fruiting dates was examined using a distance weighting smoothing technique (lowess) followed by Pearson correlation. Stepwise multiple regression was used to determine which months displayed a significant relation with average fruiting date of every species, across the 56 y. Mean monthly temperature and rainfall data were obtained from Southampton Weather Centre (www.metoffice.gov.uk/climate/uk/stationdata/southamptondata.txt), supplemented by

personal observations from 2000 when the station closed. A heterogeneity of regression test was used to compare slopes of average fruiting date v. year in the comparison of mycorrhizal species in deciduous and coniferous forests. A complete list of species used in the analysis may be obtained from the correspondence author (a.gange@rhul.ac.uk).

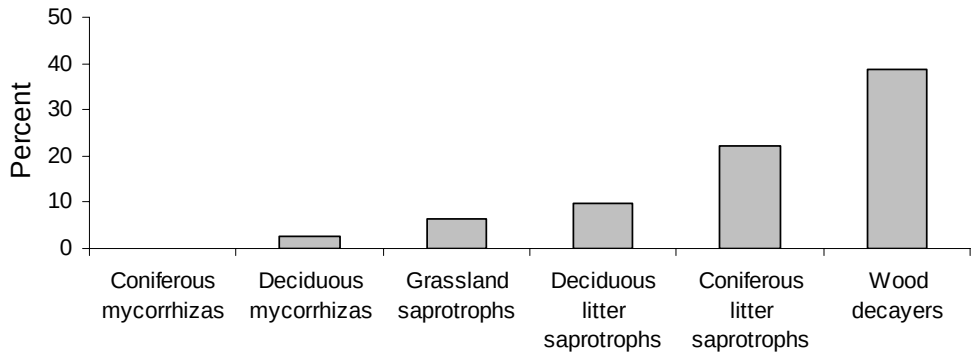

Fig. S1. Since 1975, many fungal species have started to fruit twice a year. Bars represent the proportion of species in each habitat group that, before 1975, were not recorded as fruiting in spring, but after this time did so in at least one year. 1975 was the first year in which spring fruiting of any species occurred.

Reference

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