Mushroom fruiting and climate change

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Many species of fungi produce ephemeral autumnal fruiting bodies to spread and multiply. Despite their attraction for mushroom pickers and their economic importance, little is known about the phenology of fruiting bodies. Using ≈34,500 dated herbarium records we analyzed changes in the autumnal fruiting date of mushrooms in Norway over the period 1940–2006. We show that the time of fruiting has changed considerably over this time period, with an average delay in fruiting since 1980 of 12.9 days. The changes differ strongly between species and groups of species. Early-fruiting species have experienced a stronger delay than late fruiters, resulting in a more compressed fruiting season. There is also a geographic trend of earlier fruiting in the northern and more continental parts of Norway than in more southern and oceanic parts. Incorporating monthly precipitation and temperature variables into the analyses provides indications that increasing temperatures during autumn and winter months bring about significant delay of fruiting both in the same year and in the subsequent year. The recent changes in autumnal mushroom phenology coincide with the extension of the growing season caused by global climate change and are likely to continue under the current climate change scenario.

phenology | global warming | herbarium data | fungi | agarics

Phenological changes are among the most sensitive ecological responses to changing climate (1–3). The observed extension of the average annual growing season in Europe by nearly 11 days since the early 1960s (4) has been followed by rapid and recent changes in plant flowering time (5–8) and earlier spring migration in several bird species (9). In a recent study from the United Kingdom, it was reported for a set of mushroom species that fruiting on average started earlier and ended later in the season in recent years than 20 years ago, i.e., that the fruiting period has been greatly extended (10). These changes were linked to increased temperature and rainfall in August and October, respectively (10).

Most fungi produce ephemeral fruiting bodies that can be observed only for a few days each year, which makes phenological data difficult and time-consuming to obtain. However, because of the short endurance of the fruiting bodies, collection time is a good estimate of fruiting time. A potential source of phenological information for this group of organisms is therefore herbarium collections, which, although sampled in a nonsystematic manner, share properties with random sampling processes. Herbarium data can enable us to understand and predict climate-induced ecological changes in the future by understanding how climate has affected ecological processes in the past. Several studies have already documented that herbarium collections may represent a valuable source of long-term and reliable phenological information (e.g., refs. 7 and 8).

Our study of temporal trends in fruiting phenology is based on >34,500 herbarium records collected in Norway during the period 1940–2006 and representing 83 agaricoid (mushroom) species [supporting information (SI) Table 1]. By thorough analyses of these data we aim to establish quantitative relationships between climate (and climate change) and fungal autumnal fruiting time in Norway.

Results and Discussion

In an analysis of variance, the observed variation in fruiting dates can be partitioned into between-species differences (15.8%), variability within species between years (25.9%), and variability within species within years (58.3%). Using generalized additive models (GAMs) (11) (see below and SI Table 2 for model descriptions), we find that geographic differences in fruiting time (across all species) explain 3.5% of the total variation, that temporal trends (across groups of species) explain 3.9% of the variation, and that 7.2% of the variation can be attributed to shared responses of species to interannual variability in temperature and precipitation (no temporal trend term in the model) ($P < 0.001$ in all cases; bootstrap tests).

Mushroom fruiting date changed considerably during the period 1940–2006, with earlier fruiting in the early years (1940–1950) and later fruiting in the last 15 years (Fig. 1*A*). On average across the period (and across all species) there has been a delay in fruiting of 13.3 ± 1.2 days [linear rate of change per 60 years ± bootstrap standard error ($P < 0.001$); GAM, correcting for location and species effects]. Most of the shift took place between the 1980s and the 2000s [12.9 ± 1.2 days per 20 years ($P < 0.001$); analysis of data 1980–2006]. The displacement of fruiting date parallels the delay of other autumn events, such as leaf coloring being delayed by 4.8 days in Europe during the period 1959–1993 in response to climate change (4). The delay of mushroom fruiting does, however, contrast with the general climate-induced advance in plant fruiting and ripening (1), suggesting that constraints on fruiting differ between fungi and plants.

Fruiting was more strongly delayed for the early autumnal fruiters, as revealed by a continuous interaction term fitted between initial fruiting day (1940–1959) and year (Fig. 1*B*). Whereas fruiting of early fruiters was delayed by >30 days over the entire period, late fruiters had no fruiting-time delay. This accords with a highly significant linear relationship between the initial (1940–1959) mean day of fruiting for each species and the displacement of fruiting time from 1940 to 2006 (Fig. 1*C*). Studies of spring phenology in plants have also shown differences between "early" and "late" species in their response to climate change (5, 12). The stronger delay for early fruiters compared with late fruiters implies that the start of the fruiting season has been delayed while the end has remained more or less unchanged. Thus, the mushroom fruiting season in Norway has become progressively more compressed into late autumn in Norway. A decrease in residual variation (most at the within-species within-year level; restricted maximum-likelihood analysis) with time also indicated that the length of the overall fruiting

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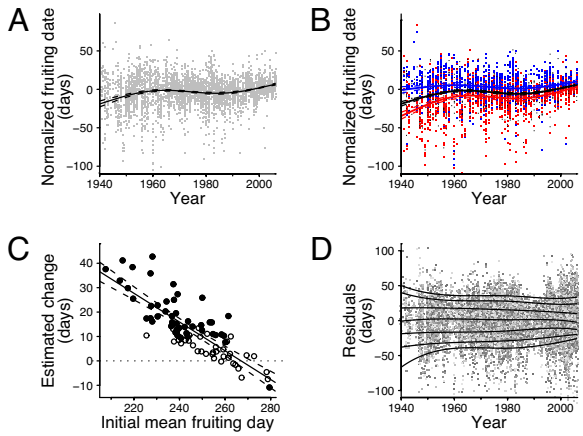

Fig. 1. Temporal variation in fruiting during the period 1940–2006. (*A*) Diagram showing temporal changes in seasonal fruiting time during the period 1940–2006. Lines indicate fitted year effect with 95% bootstrap confidence limits from a GAM in which species and location effects were accounted for. The trend was modeled as a smooth effect of time and was significantly positive ($P < 0.001$, bootstrap test). Points indicate partial residuals averaged for each species and year combination. (*B*) Changes in fruiting during the period 1940–2006, partitioned on early (red; 28 species), middle, (black; 27 species) and late (blue; 28 species) fruiters. Lines indicate fitted year effects with 95% bootstrap confidence limits (for the median of the initial mean fruiting dates within each group) from a GAM in which species and location effects were accounted for. The trend was modeled as a tensor-product smooth function of time and initial fruiting day. This model provided significantly better fit to the data than the model with a common trend for all species ($P < 0.001$, bootstrap test). Points indicate partial residuals averaged for each species and year combination. (*C*) Displacement in fruiting time during the period 1940–2006 for the 83 fungal taxa related to initial (1940–1959) mean day of fruiting of each species. Displacement in fruiting (per 60 years) was calculated for each species separately by using GAMs with linear time effects and the geographic effects accounted for by smooth functions of longitude and latitude (thin-plate regression spline with maximally 11° of freedom). Filled points indicate statistically significant effects ($P < 0.05$, bootstrap tests for each species). Lines indicate linear regression line ± 1.96 standard error (across species). (*D*) Residuals from the model shown in *B*. Lines indicate quantiles (5%, 10%, 25%, 50%, 75%, 90%, and 95%) as estimated by quantile regression (23, 24). The standard deviations of the residuals within years were negatively correlated with year (Pearson's correlation coefficient, $r = -0.46$, 95% bootstrap c.i. = −0.64, −0.26), as were the standard deviations of the raw observations ($r = -0.47$, c.i. = −0.63, −0.28).

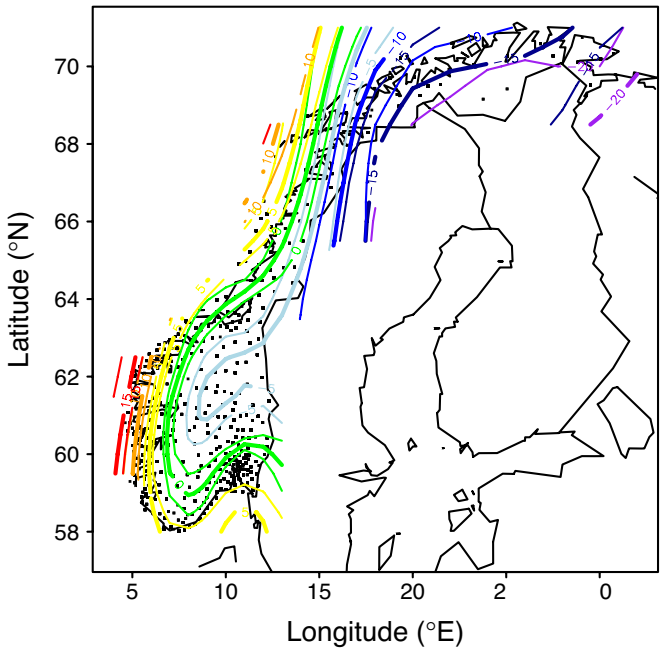

Fig. 2. Spatial patterns in mean day of fruiting of 83 fungal species in Norway. The isoclines (lines of different colors) represent iso-lines with 95% bootstrap confidence limits. The effect of geographic location was estimated as smooth functions of longitude and latitude (thin-plate regression spline with maximally 11° of freedom) by using GAM also accounting for effects of species and temporal trends (Fig. 1*B*).

season has been compressed (Fig. 1*D* and *SI Text*). Our results contrast with Gange *et al.*'s recent finding that the mushroom fruiting season has expanded in both directions in the United Kingdom (10). We see no obvious reason why first and last fruiting dates in the United Kingdom should show trends different from the early and late quantiles of Norwegian mushroom fruiting dates (Fig. 1*D*), nor are we aware of differences in the mechanisms controlling mushroom fruiting between the United Kingdom and Norway. Studies of the cues and constraints that govern fungal fruiting might clarify this issue. Cues might relate to autumnal events that occur later than before, whereas constraints on resource acquisition and achieving "fruiting potential" might be fulfilled earlier when the climate is milder. In many mushrooms, fruiting can be induced experimentally after vegetative growth by reducing the temperature by at least 5°C (13), and this might be an important environmental cue that has been delayed because of global warming.

Geographic location was also found to be highly important for fruiting date. Fruiting bodies typically appear considerably earlier (in the range of 10–20 days) in northern, continental, and alpine regions of Norway compared with more southern and oceanic regions (Fig. 2). This latitudinal pattern follows general trends well known from plant phenology (14). However, we did not find significant dependencies of temporal changes in fruiting date on location (SI Table 2).

We found no relation between trends in fruiting time and fungal feeding mode, i.e., whether fungi live in symbiosis with plants (ectomycorrhizal mode) or feed on dead organic matter (saprotrophic mode) (SI Table 2). Gange *et al.* (10) found delayed fruiting only for mycorrhizal fungi living in association with deciduous trees but not for fungi associated with conifers (which lack a concentrated period of leaf shedding). Unfortunately, our herbarium data do not allow a similar comparison.

Temperature and moisture are exogenous key factors known to influence the production of autumnal fruit bodies (15). We analyzed the effects on fruiting time of monthly regional anomalies in temperature and precipitation from June the preceding year to November the immediate year. Our results suggest that high temperature during November the preceding year, high precipitation during July the preceding year, and high temperatures during February, August, and October (the current year) are associated with delayed fruiting (Fig. 3). Furthermore, high temperatures during May and June, high precipitation during June and October, and intermediate amounts of precipitation during November (all factors referring to the current year) are associated with earlier fruiting (Fig. 3). Worth noticing is that the overall year effect (Fig. 1*A*) was no longer statistically significant when added to the best model with climatic predictors (SI Table 2). Hence, the documented overall year effect is explainable as a direct effect of significant increases of winter and autumn temperatures in Norway during the last decades (SI Tables 3 and 4).

It might be claimed that our results have been derived from biases in the data. However, we find it most unlikely that sampling bias, for which herbarium data may be criticized on theoretical grounds, can account for the observed delay in fruiting. For our data to be biased with respect to fruiting time, a temporal shift in collecting effort toward later in the autumn

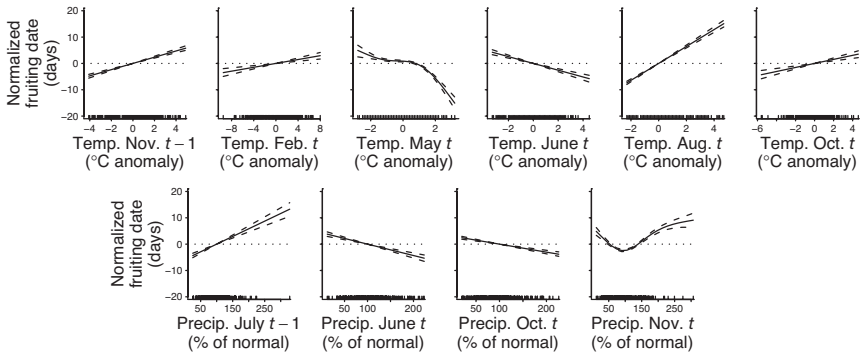

Fig. 3. Climatic effects on interannual changes in fruiting of 83 fungal species. Temperature and precipitation variables are referring to either the preceding year ($t - 1$) or the same year (t) as fungal fruiting. The climatic effects shown were estimated as linear or smooth terms in one GAM also accounting for location and species effects (SI Table 2). Whole and broken lines indicate fitted partial effects with 95% bootstrap confidence limits. The tick marks on the x axis show the location of the covariates (see also SI Fig. 4, showing partial residuals).

would have to have taken place during the period 1940–2006, most dramatically during the last 20 years when the most dramatic changes in fruiting time have taken place. It seems difficult to imagine any rational reason for such a change of behavior among fungus collectors. Furthermore, we are unable to see how sampling bias possibly could lead to significant associations between monthly climate variables and fruiting time, especially with time lags. Consequently, we think that the delay in fruiting is most parsimoniously explained through the documented effects of climate.

Through our analysis we have demonstrated changes in the temporal pattern of fungal fruiting in Norway during the period 1940–2006 that most likely are responses to climate change. Worth noticing is that the accelerated delay of fruiting in the last 20 years has coincided with dramatic global warming (16). We predict that the projected rise of global temperatures by up to 4°C by 2100 (16) will have drastic effects on fungal fruiting phenology. Because fruit bodies function as habitat and diet for many organisms, these changes may have profound side effects.

Materials and Methods

Data. Data for agaricoid species (mushrooms) with at least 250 entries in the Norwegian Mycology Database (Natural History Museum, University of Oslo) and with mainly autumnal fruit bodies were included in the study ($n = 83$ species) (SI Table 1). Only herbarium records with a proper dating (day) and geographic localization (municipality) were used for analyses. The approximate geographic positions of the records were obtained by allocating geographic coordinates for the municipalities to the records. Categorical information for the species feeding mode (saprotrophic or ectomycorrhiza) was also included. The number of records analyzed for each species ranged from 226 to 945; the total number of records was 34,528. Climate data for monthly temperature and precipitation anomalies in Norway's five main regions, for the period 1939–2006, were obtained from the Norwegian Meteorological Institute.

Statistical Analyses. We used the GAM implementation of the ''mgcv'' library of R (11). To compare competing models we computed genuine cross-validation (CV) errors, models with lower CV having higher out-of-sample predictive power. Because of within-year correlations in the response variable, CV was calculated by leaving data for 1 year out at a time. Outlier observations ($n = 60$), identified by using Grubb's test (17) on the residuals from a GAM accounting for species and location effects, were removed before final analyses. All outlier observations were records made before day 155 (June 4). A total of 34,468 records (after outlier exclusion) for all of the 83 species were analyzed in one model with collection time (reflecting the time of fruiting) as response. Thus, we did not use first/last observations as, e.g., Gange *et al.* (10) did, but instead included all records throughout the entire fruiting season, revealing trends both in mean fruiting date and in the variability around these trends. Differences between species in mean fruiting time were accounted for in all models, as were location effects. Location effects (as shown in Fig. 2) were assumed to be similar across species and were modeled by a thin-plate regression spline of longitude and latitude (maximally 12 knots, i.e., 11° of freedom). Temporal trends were modeled as either linear or smooth effects (natural cubic splines with maximally 4 knots) of year (1940–2006). Possible differences in temporal trends between (*i*) different regions (central, east, north, south, and west Norway), (*ii*) species groups defined by feeding mode (saprotrophic and ectomycorrhiza), or (*iii*) species groups characterized by the initial (1940–1959) mean day of fruiting (the 28 earliest-fruiting species, the 27 intermediate-fruiting species, and the 28 latest-fruiting species) were accounted for in models with group-specific year terms (i.e., with 5, 3, or 2 smooth year terms instead of 1). A continuous interaction between initial fruiting day and year was modeled by a tensor-product smooth function constructed from linear combinations of terms that were cubic regression spline basis functions of the two variables (each with maximally 4 knots) (11). CV showed that only the interaction terms including initial fruiting day and year improved the model (SI Table 2). Accordingly, results from the continuous interaction model, which had the lowest CV prediction error, are shown in Fig. 1*B*. Data points are colored by intervals of initial fruiting date as detailed in the figure legend.

A separate model was fitted to identify climate variables accounting for interannual variation in fruiting. Linear effects of 36 different climate variables were considered (monthly regional anomalies in temperature and precipitation from June the preceding year to November the current year). Starting with the full model, terms were removed until the model with the lowest CV prediction error was found. CV prediction error was reduced further by substituting two of the selected linear climatic effects with smooth terms and subsequently removing two more linear terms. We also explored the possible direct or lagged effects of the North Atlantic Oscillation (NAO) using the PC-based NAO index described in refs. 18 and 19 (www.cgd.ucar.edu/cas/jhurrell/indices.data.html#naopcdjfm), but we found this to have lower explanatory power than the precipitation and temperature indices (results not shown). Finally we tested for linear interaction effects between the selected climatic variables and feeding mode or initial fruiting time and for the combined effects of climatic variables and year. We found no significant interactions between the climatic variables and feeding mode. We found evidence for a negative interaction between initial fruiting day and temperature in February and October (SI Table 2), suggesting a stronger response of early fruiters to these climate variables. However, these interaction effects did not fully explain the stronger year effect of early fruiters, because adding an interaction term between year and initial fruiting day improved the predictive power of the model (SI Table 2). In contrast, the model with only climatic variables was not improved by adding a smooth year effect (SI Table 2), suggesting that the overall temporal trends are indeed explainable by the measured climatic variables.

The statistical significance of terms and confidence intervals were computed by using a modified wild bootstrap approach (20, 21), as described in ref. 22, which accounted for both heteroscedasticity and within-year correlation of residuals. When calculating the significance of terms, bootstrap data sets were constructed from residuals and fitted values from models without the given terms, and the increase in variance explained (R^2_{adj}) by including the given terms was used as test criterion. When calculating the significance of the interaction between initial fruiting day and year, initial fruiting day was recalculated for each bootstrap sample, thus accounting for bias resulting from one of the predictor variables being derived from the response variable.

A quantile regression analysis, using the Frisch–Newton interior point

method and cubic splines with 8 knots, was performed with the residuals from model shown in Fig. 1*B* as response (23, 24). In a separate analysis (*SI Text*), residual variance structure was analyzed by restricted maximum-likelihood methods (25) using the nlme library of R (26), selecting the most parsimonious model based on Akaike's information criterion.

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