Congruency in fungal phenology patterns across dataset sources and scales

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Abstract

As citizen science and digitization projects bring greater and larger datasets to the scientific realm, we must address the comparability of results across varying sources and spatial scales. Independently assembled fungal fruit body datasets from Switzerland and the UK were available at large, national-scales and more intensively surveyed, local-scales. Phenology responses of fungi between these datasets at different scales (national, intermediate and local) resembled one other. Consistently with time, the fruiting season initiated earlier and extended later. Phenology better correlated across data sources and scales in the UK, which contain less landscape and environmental heterogeneity than Switzerland. Species-specific responses in seasonality varied more than overall responses, but generally fruiting start dates were later for most Swiss species compared with UK species, while end dates were later for both. The coherency of these results, across the data sources, supports the use of presence-only data obtained by multiple recorders, and even across heterogeneous landscapes, for global change phenology research.

Keywords

climate, fungi, phenology, multisource data, seasonality, spatial scale

Introduction

Long-term species observation records are commonly used in ecology to determine changes in phenology that are correlated with global change. Historical datasets (maintained by museums and scientific societies) which note the presence of a particular species in a particular locality are considerably more spatially and temporally comprehensive than are the data currently available in published scientific literature, atlases and websites (Boakes et al. 2010). The former sources are considered the 'gold-standard' for phenology research due to their high accuracy when processed appropriately to reduce biases (Davis et al. 2015). For some organisms (e.g. many plants and vertebrates) observations are relatively straightforward and ground-truth methods can be utilized to verify historical dataset accuracy (Primack et al. 2004, Robbirt et al. 2011, Calinger et al. 2013). However, for other organisms, such as fungi, it is difficult because they are largely hidden from sight. A fruit body indicates presence, but absence of a fruit body does not imply absence of the fungus, whose mycelium may remain hidden in soil, wood or within whatever it is feeding on. DNA-based analyses may better solve this problem in the future, but currently there are no comparable long-term large-scale datasets with highly precise and also widely distributed taxonomic and temporal resolution data available for DNA-based analyses. Large numbers of macroscopic fruit body records are cost-effective to obtain, and have greater and/or more positive public perceptions, hence their major contributions by citizen scientists to ecological data (Halme et al. 2012). For these reasons, the scientific value of these types of records to ecological research is unlikely to decrease in the near future. In fact, as the ecological and economic benefits of understanding climatic change effects on organisms outweigh the potential pitfalls of multi-source observational data, these data are likely to increase in their ecological use (Graham et al. 2004, Halme et al. 2012, Miller-Rushing et al. 2012).

While the importance of presence-only datasets to science is unequivocal, there are nonetheless numerous potential biases that may affect the results and interpretation of analyses of such data, even after parsing to reduce addressable biases (e.g., Boakes et al. 2010, García-Roselló et al. 2015, Andrew et al. 2017). Direct assessments of biases between differing sources of presence-only datasets have occasionally been investigated (Davis et al. 2015). Difficulties in recording methods can arise as a result of multiple recorders (recorder bias), from recording at different scales (spatial bias), or due to inequalities in timespans or temporal sampling intensities (temporal bias) (Boddy et al. 2014, Davis et al. 2015). Further issues within these groupings include: taxonomic misidentifications; bias in recording favoured taxonomic groups; tendencies to under or over-report very common or rare taxa; lack of a standardised sampling regime and collection effort; temporal and spatial gaps in records; and preference for certain recording sites (Graham et al. 2004, Halme et al. 2012, Boddy et al. 2014, Davis et al. 2015, Isaac et al. 2015).

Recent approaches to minimizing bias in presence-only data have focused on statistical manipulations or data filtering procedures prior to analysis (Geldmann et al. 2016, Stropp et al. 2016). While helpful up to a point, these can drastically reduce the number of samples and, thus, the reliability of the data, and introduce further statistical problems (Isaac et al. 2015). There are, then, reasons to forego bias removal techniques. The question remains in these cases: how robust are results when data are minimally treated for bias? This is important to understand, as we must endeavour to explain ecology within the context of global change with what data are available, which will likely never have all potential biases completely removed. While resources are available to help with concern over data quality and filtering, there is also considerable ambiguity to the best practices (e.g., Graham et al. 2004, Boakes et al. 2010, Robbirt et al. 2011, Miller-Rushing et al. 2012, Davis et al. 2015,

García-Roselló et al. 2015, Isaac et al. 2015, Geldmann et al. 2016, Stropp et al. 2016). Thus, here we shift the focus from exploring bias techniques to whether ecologically informative results can be gained across data sources and scales, despite any potentially remaining biases (after basic filtering of multi-source data; e.g., Andrew et al. 2017).

In this study, we make direct comparisons of fungal fruiting phenology across datasets collected in different ways, with different recorder efforts and at different temporal and spatial scales. We focus on data of fruiting basidiomycetes, and more specific agaricoid fungi that typically produce ephemeral fruit bodies, so that the date of a record is a good approximation of fruiting. While we follow the standard primary filtering steps to reduce biases as far as possible, we also purposefully have not drastically modified the data. Our goals are to assess the robustness of phenology results across multiple datasets and scales when the data are minimally treated for bias.

The analysis includes: (1) national scale datasets from the United Kingdom (1950-2008) and Switzerland (1975-2006) compiled from data submitted by multiple recorders, and collected in a non-structured manner in space and time, but with greater focus on the autumn fruiting season; (2) intensively collected local datasets from a ca. 3000 km^2 area in the UK with a similar number of recording occasions throughout the year (1950 -2008), and (3) from a < 1 km^2 forest plot in Switzerland which was exhaustively sampled throughout the summer and autumn fruiting season (1975-2006); and (4) intermediate scale datasets extracted from the national datasets. For the UK and provided mostly as supplemental material (as results were similar and only added complexity), an additional local-scale dataset was analysed which was extracted from the national-scale data (see Material and methods).

Dataset comparisons and hypotheses were as follows: (1) despite considerable variability derived from multiple collectors, the phenological trends in national datasets will be similar to those in the intensively collected datasets; (2) the comparability of all datasets from a single country will be relatively high (i.e. greater than by chance), and higher than between countries; (3) within-country datasets of similar-scaled sources will be more correlated than differently-scaled sources. Climatically-driven temporal effects on fungal fruit body seasonality (start, end, and mean fruiting days) were determined for all fungi as well as subsections by fungal nutritional modes (saprotrophic versus ectomycorrhizal fungi), thus placing these results within a global-change biology context.

Methods

Datasets

Four data sources were used in this study, and are described in detail below. All dataset sources had independent origins, but were expanded into six main dataset scales for comparison (Table 1, Figure 1), plus one additional dataset for comparison within scales (supplementary material; the results added too much complexity without any novelty to the overall results). Standard dataset combination and bias removal techniques first homogenized all of the data, and quality, across sources (Andrew et al. 2017). For example, the taxonomy across datasets was streamlined, temporal resolutions were equalized, discrepancies and duplicates were removed, records with dubious or missing data removed and georeferences verified.

The UK national (and matching, extracted intermediate) scale dataset was derived from multiple sources, including individual contributions, foray lists and fungarium data from the Royal Botanic Gardens, Kew, United Kingdom. Data were from The Fungal Records

Database of Britain and Ireland (FRDBI; www.fieldmycology.net; http://www.frdbi.info/), available from 1760 to 2014, but only data from the mainland countries of England, Scotland and Wales, a region of approximately 209,331 km^2, were used. For the current study, data were limited in temporal (1950-2008) and spatial ranges, plus taxonomic groups to match the local dataset (see below).

The Swiss (CH) national (and intermediate) scale dataset was also a compilation of individual contributions, forays, scientific surveys and fungarium data. It is managed at the Swiss Federal Research Institute WSL in Birmensdorf/ZH (www.swissfungi.ch). Data are available from 1904 to 2014 across the country of approximately 41,285 km^2. Again, a narrower dataset timespan (1975-2006) and taxonomic coverage was used to filter and match the national and local data sources (Table 1).

In the UK, a local scale dataset (called the Gange dataset) was earlier compiled based on weekly fruiting records across 1,424 locations within a 30-km radius (2,828 km^2) of Salisbury, Wiltshire, United Kingdom (Figure 1). Now part of the UK national dataset, it was separated from that data for use as a local dataset (those records then removed from the national and intermediate data to avoid duplication). Fresh fruit bodies were recorded each week of every year between 1950 and 2008 from haphazardly selected sites (Gange et al. 2007, Boddy et al. 2014). The spatial coverage of the UK local dataset was much larger than the CH local dataset, but for simplicity both are referred to as local throughout the paper. The spatial areas of each comprise less than 2% of their matching national dataset ranges (Table 1).

The Swiss local scale dataset (called the La Chanéaz dataset) was created from a weekly fruit body monitoring project running from 1975 to 2006 at the La Chanéaz Fungus Reserve (Swiss Federal Institute for Forest, Snow and Landscape Research WSL) near Payerne, Switzerland (Figure 1). Five 300 m^2 plots were surveyed throughout the growing season of May to November (Egli et al. 2010). These data were collected independent of the national-scale dataset.

In addition to the four independent datasets described above, two intermediate scaled subsets were extracted from the national-scale datasets. These data were not removed from the national datasets, as their sources were the same (unlike the local scale datasets). As with the local data, the spatial areas of the intermediate datasets did not match between the countries but instead were determined by altitudinal or political boundaries inherent to each dataset (vice counties for the UK, and bioregion for Switzerland). Our purposes were not directly based on specific comparisons of scale sizes to phenology effects across time, but rather to comparisons of reported phenology responses across datasets with differing scales and/or sources. Thus, discordance between the regional and local delimitations between the countries did not affect our conclusions.

Data for the intermediate UK dataset were from the UK-national dataset, but limited to the vice counties of and immediately surrounding the UK local scale (Gange) dataset (Figure 1). This subset provided an intermediate scale level for comparison between local and national scales (Table 1), with expectations for potentially greater similarity to the local scale than the national scale data.

For the Swiss intermediate scale data, from the national scale dataset, the data were extracted corresponding to the matching bioregion of the local scale (La Chanéaz) data, i.e. the Swiss (Central) Plateau (Schweizer Mittelland). This geographic area covers approximately 12,385 km^2 and addressed our interest into regional climatic influences causing greater similarity in phenology responses across dataset sources, i.e. was not created for direct spatial scale comparisons by datasets, which would require a different study than this.

Finally, one more dataset was extracted from national data. Given our curiosity as to how phenology responses varied at the finest scale, i.e. corresponding to the independent local dataset, a second dataset was extracted from the UK national scale data, limited to the same vice counties from which the Gange local dataset was collected, but covering the whole of these vice counties, i.e. a slightly larger area than the Gange local dataset. These data overlapped in spatial area but not in data source. As expected, results between the local Gange dataset and this matching local dataset were very similar. Thus, to reduce complexity and redundancy in the results, only those for the Gange dataset are presented (but see Supplementary material for results on this second local scale dataset, extracted from the national UK data).

Dataset processing and bias reduction

As mentioned previously, the data we utilized had already been treated to standard homogenization and bias reduction processing techniques (Andrew et al. 2017). Further temporal and taxonomic biases were removed, unique to these four datasets (and the accompanying two datasets extracted from the national data): The national datasets were first cut-down to cover the same time spans as the local scale datasets, i.e. 1950-2008 for the UK, and 1975-2006 for CH (Table 1). Taxonomies were synonymised using Species Fungorum

taxonomy (Cannon and Kirk 2007, Ainsworth 2008, Kirk et al. 2008; www.speciesfungorum.org). Only ephemeral fruiting species were retained for analysis to reduce further bias (i.e., species within the Agaricales, Boletales, Geastrales, Gomphales, Phallales and Russulales). These steps reduced the number of records and species for both countries (Table 1). Overall, however, our goal was to minimally treat the data for bias; hence, the paucity in processing steps.

Records distributions within each dataset and scale were evenly distributed across each survey area (Andrew et al. 2017) though they differed between datasets: for the UK, national and intermediate dataset densities were overall ca. 2.9 and 2.6 records/km^2, while for the Swiss national dataset, density was slightly higher at 3.7 records/km^2 (Table 1). Again, our purpose was to gauge comparability in results when such differences between datasets remained intact and, furthermore, sample intensity was statistically taken into account in some of the analyses.

Statistical analysis

Changes in phenology were first directly assessed by Pearson correlation analyses performed between all combinations of national, intermediate and local scale data for, separately, Switzerland and the UK. Analyses were performed on the mean ordinal fruiting days across the whole timespan for all species (the start date was 01 March to reduce the influence of the previous fruiting season extending into January and February (e.g., Kauserud et al. 2012)). Available as supplementary material (as they were similar but more complex renditions), the same analyses were conducted at the inter-annual level for each of four of the more commonly recorded species across datasets and scales (two saprotrophs, *Hypholoma fasciculare* and *Rhodocollybia butyracea*, and two ectomycorrhizal taxa, *Laccaria laccata*

and *Russula ochroleuca*; Table 2). The choice of the four species (instead of more) balanced complexity in analyses with representation of both mycorrhizal and saprotrophic nutritional modes.

We analysed phenology trends following the methods of Kauserud et al. (2012): Three annual fruiting summary statistics (start, mean, and end) were applied to: (i) generalized least-squares regressions (GLS) that extracted the estimated year effect for each species within each dataset scale (Wood 2006) and (ii) linear mixed-effect models (LME) that focused on broad-scale trends across dataset scales and nutritional modes for all species within each dataset (Pinheiro and Bates 2000, Myers et al. 2002). Thus, we obtained information on whether fruiting season start date and length shifted by (i) species for each dataset scale and (ii) an overall annual trend with species analysed together. Variability in sampling intensity (i.e., another bias source that must be controlled for) was handled by weighting the number of occurrences (N). Potential nonlinear bias was treated by including a lm(N + 1) term as a fixed effect, in addition to a year effect. An autoregressive (AR) 1 procedure (Pinheiro and Bates 2000, Zuur et al. 2009) included the residual temporal dependencies into the variance estimates, as the data were time series with regular intervals. An additional taxonomic constraint was included in the LME analyses that provided estimates to measure the magnitude of genera and, within, the species in terms of mean timing and change within time. Nutritional modes were included as a term using a residual variance estimate in the relative difference between saprotrophic and ectomycorrhizal (ECM). For further details, refer to Kauserud et al. (2012). All statistical analyses were conducted in R version 3.2.2 (R Core Team 2015) with the use of the {mgcv} package.

Results

Overlap in species across data sources and scales

For the six selected orders (Agaricales, Boletales, Geastrales, Gomphales, Phallales and Russulales), 2,543 species appeared in the Swiss datasets, of which 2,531 (99.5%) were represented in the national-scale dataset (Figure 2). Only 13 species (0.5%) were unique to the Swiss local-scale dataset (La Chanéaz) that had 332 species in total. 1,520 species (59.7%) were unique to the Swiss national-scale dataset, while 1,838 (72.6%) of the species present in the Swiss national-scale dataset were subsampled into the intermediate-scale dataset. The uniqueness of those species in the local dataset is likely a better measure of taxonomic bias remaining within the data than of actual uniqueness in comparison to elsewhere in the country. For the UK datasets, a slightly higher total number of species was recorded (2,861) compared to the Swiss datasets, of which 2,845 (99.4%) were present in the UK national-scale dataset. As for the Swiss data, only a small number of species (16 = 0.1%) appeared uniquely in the independent local-scale dataset (Gange) for the UK, this dataset including 1,120 species in total. The low number of unique values positively reflect the dataset qualities, showing very low remaining, unaccounted for, taxonomic bias. For the UK, 2,307 species were subsampled into the intermediate-scale UK dataset, representing 80.6% of all species in the national scale dataset. Commonly the top recorded taxa at the national and intermediate scales were also in the top twenty of the local scale data (Table 2).

Fungal phenology across data sources and scales

In terms of phenology, R^2 values for the mean fruiting day, when all species were included (i.e. the non-individual species responses), were above 0.3 for all scale comparisons and generally higher than 0.4 (Figure 3, Supplementary material 1, 2). Between the local and national datasets for each country, R^2 values were the lowest. In contrast, the highest R^2 values differed between country. A high R^2 value (of 0.72) in fruiting time was observed

between the Swiss local-scale versus intermediate-scale datasets (Figure 3A). For the UK, the greatest correlation was between the intermediate-scale and the national-scale dataset (R^2 = 0.83; Figure 3F). The correlations in the mean yearly fruiting time across scales for the top four species were substantially lower, with widely varied estimates between dataset scale comparisons (Supplementary material 3, 4).

Fruiting season was altered in many species across the dataset sources and scales (Figure 4, Supplementary material 5). Especially the end of the fruiting season has become more delayed for many species (seen in a positive 'exit day' slope), and was highly consistent across all dataset sources and scales (Supplementary material 6). In contrast, across scales within Switzerland the start date more often shifted to delayed (seen in a positive 'entry day' slope), while in the UK it more often shifted to earlier fruiting (a negative 'entry day' slope). Across all scales, there were fewer phenology shifts to a later start day and earlier end day, meaning most species did not exhibit a seasonal reduction in the extent of their fruiting period. Instead, and across all scales and both countries, most species expanded their fruiting season through either earlier start dates, later end dates, or the combination of both. This pattern also held in the across-species analyses (Figure 5, Supplementary material 7). Earlier-season (2.5^{th} percentile) fruiting became even earlier with time for the dataset scales in both the UK and Switzerland. Later-season (97.5^{th} percentile) fruiting likewise lengthened across all dataset scales and sources, and generally the mean fruiting day either remained relatively stable or became later. All these results correspond to a general extension in fruiting season start and duration, with only the Swiss local dataset deviating for certain responses (i.e., Figure 5b). Saprotrophic fungi had a more pronounced seasonal shift in comparison to ectomycorrhizal fungi (Figure 5).

Discussion

The datasets compared here originally varied substantially in many aspects (even after accounting for the minimal, standard set of biases to allow for comparisons). Could similar patterns in correlation and phenology trends exist, despite these differences? We affirm that trends are directionally similar with high correlation values for species-wide comparisons (Figure 3), upholding all three of our hypotheses. Even more striking, phenology patterns across scales were extremely consistent in terms of fruiting start and end dates (Figure 4) as well as temporal trends in earlier (2.5^{th} percentile), mean and later (97.5^{th} percentile) fruiting season days (Figure 5). This is highly important to establish, as studies that investigate climatic effects on scale-dependent processes, e.g. niche conservatism (Amano et al. 2014), are thus suitable to be extended to combined multi-source observational / fungarium data.

Care must be taken, however, to establish how the data were analysed prior to comparing results across scales and sources. For example, although we can accept our first hypothesis, there was never a complete correlation (1:1) in the fruiting day comparisons between dataset scales and types, though the correlations were consistently positive. This demonstrates how general trends can be expected to be relatively similar with such 'simple' statistical comparisons (Figure 3), though more similar when data attributes relating to, for example, sampling intensity and temporal dependencies (Wood 2006, Zuur et al. 2009, Kauserud et al. 2012) are taken more fully into context (Figure 4, 5).

A more straightforward approach to analysis can allow greater robustness contingent on the spatial scale and environmental heterogeneity, with greater deviance in comparability either at extremely precise resolutions and/or within more heterogeneous environments (i.e., we can accept our second and third hypotheses). For example, often the UK data were closer to a 1:1

ratio than were the Swiss data, which exhibited greater variability in number of records (Figure 2) and, hence, generally lower correlation values (Figure 3). The spatial scale of the smallest Swiss dataset, the local-scale (La Chanéaz) dataset, at less than 1 kilometre is extremely small in comparison to all other datasets (Table 1). Likely the high specificity of this local scale dataset within a highly heterogeneous landscape (due to altitudinal changes) explains much of reduced correlation with the larger scale dataset.

Biogeographic region (and its accompanying altitude, climatic regime and habitat availability) is important in determining fruiting responses than is scale alone. This is demonstrated by the better correlation of the intermediate scale data, extracted from the national datasets, with the local scales (Figure 3; third hypothesis accepted). The greater environmental variation in Switzerland, due largely to the Alps, appears to lead to poorer correlations across spatial scales and, at least partly, explains the greater number of unique taxa at the national scale (59.7%) than in the UK (17.8%), a more environmentally homogenous country (Figure 2). In contrast, the local-scale datasets for the UK exhibited similar trends to the intermediate and national scale data (Figure 3, Supplementary material 1, 2). Our original hypotheses did not cover completely all potential results: Environmental heterogeneity as well as spatial scale can affect response results, especially with less complex statistical approaches.

There are other considerations that our hypotheses did not cover: first, the comparability of phenology results are more robust across species than at the species-specific level. This could be at least part due to a difference in statistical power and sample size in the less replicated species-specific analyses compared to analyses across the whole. Thus, a point of concern is with regard to individual species-specific responses, often conducted due to a greater

assurance of coverage within a given dataset (e.g., Primack et al. 2004, Robbirt et al. 2011, Davis et al. 2015). Correlations for each of the main four fungal species and their yearly number of records were more variable than analyses across all species combined, perhaps capturing temporal variability lost in the other analyses (Supplementary material 3, 4). While our results suggest similar responses of fruiting metrics across dataset spatial scales and species (Figure 3), care must be taken when analysing and interpreting species-specific responses, especially at the annual temporal scale. Species-specific phenology responses to larger- versus more local-scale correlations can vary due to environmental conditions (Frederiksen et al. 2004), supporting further likely causes for the more complex responses we documented at the species-level for dataset scale.

Perhaps of most interest is how the fruiting season extension, through either earlier start day, later end day, or a combination of both, for species across all scales (Figure 4, Supplementary material 5, 6) mirrors previous results (Kauserud et al. 2012). The general temporal broadening in the fruiting season across species (Figure 5) also parallels that already shown (Gange et al. 2007, Kauserud et al. 2012, Boddy et al. 2014). What is unique here is that this response is highly consistent across all dataset scales and sources, evidencing the robustness of these forms of data for phenology research. In comparison to the fruiting day correlations (Figure 3), these results exhibited more clearly similar patterns (Figure 4, 5); they more appropriately accounted for potential dataset differences (e.g., sampling intensity) while the correlations (as in Figure 3), though more intuitive to grasp statistically, failed to do so. The results verify the comparability of fruiting phenology responses across dataset regions and scales. Note that, as with the direct correlations, species-specific phenology responses were more susceptible to regional variance in landscape and climate (Figure 4) while temporal trends across species were more robust (Figure 5).

Early studies demonstrated distinct phenological effects of climate change on fungal fruiting, though results between studies/countries varied (Gange et al. 2007, Kauserud et al. 2008, 2010, 2012). One concern was that these differences arose from biases in multi-recorder national scale datasets, compared with local datasets, but this is clearly not an issue when analysed appropriately. We have shown that presence-only data can provide relatively uniform responses, in terms of correlation direction and strength, irrespective of scale. Our results corroborate botanical research (e.g., Cleland et al. 2007, Davis et al. 2015), suggesting phenology studies are impervious to (at least some) lingering potential biases in datasets. Our results also give confidence that datasets derived in different ways, from different countries (Schenk-Jäger et al. 2016, Andrew et al. 2017), will yield equivalent phenology signals. Therefore, combining datasets (and removing minimal biases as possible) and comprehensive analysis offers the unique potential to investigate fruiting responses across landscape- to continental spatial scales and within in the context of global change. Finally, we expand the conclusions of earlier studies that temporally-related climatic influences have undoubtedly impacted the fungal fruiting season, independent of geographical locality.

Authors' contributions (listed alphabetically by last name)

LB, EH, HK conceived the study

SE, AG, EG, PK, BS provided data

CA, LB, EH, HK participated in the design of the study

CA, LB, EH, HK conducted the statistical analyses

CA, LB, UB, SE, AG, HK, BS drafted the manuscript

All authors gave final approval for publication.

Competing interests

All authors affirm that no competing interests exist with respect to this manuscript.

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Figures

Figure 1

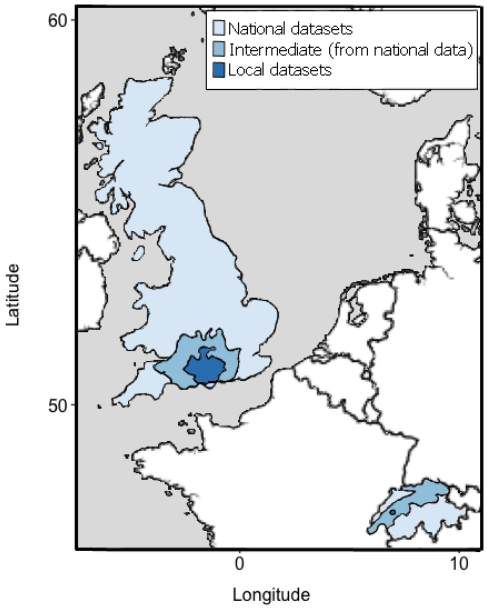

Figure 2

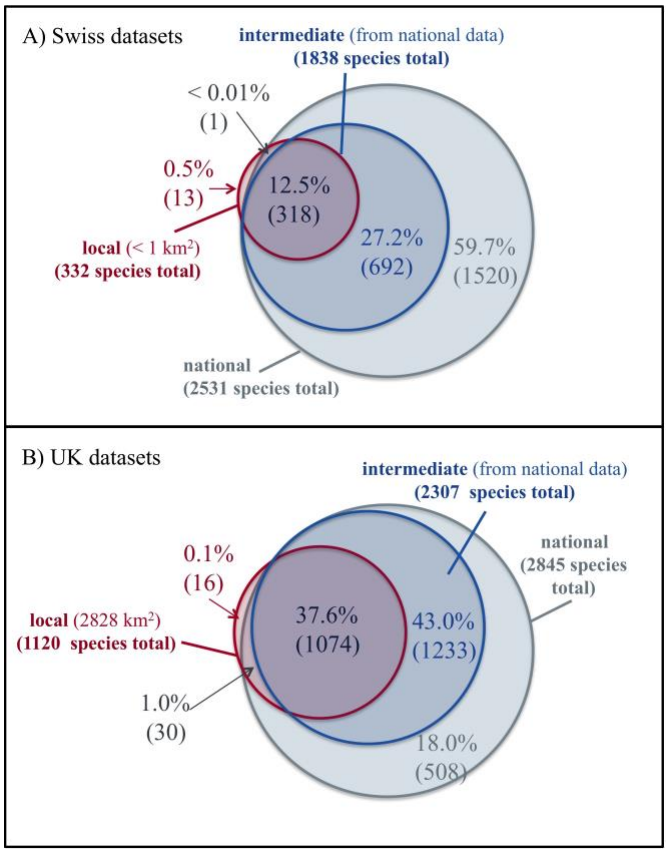
A) Swiss datasets
intermediate (from national data)
(1838 species total)
< 0.01%
(1)
0.5%
(13)
12.5%
(318)
27.2%
(692)
59.7%
(1520)
local (< 1 km²)
(332 species total)
national
(2531 species total)
B) UK datasets
intermediate (from national data)
(2307 species total)
national
(2845 species
total)
0.1%
(16)
37.6%
(1074)
43.0%
(1233)
local (2828 km²)
(1120 species total)
1.0%
(30)
18.0%
(508)

Figure 3

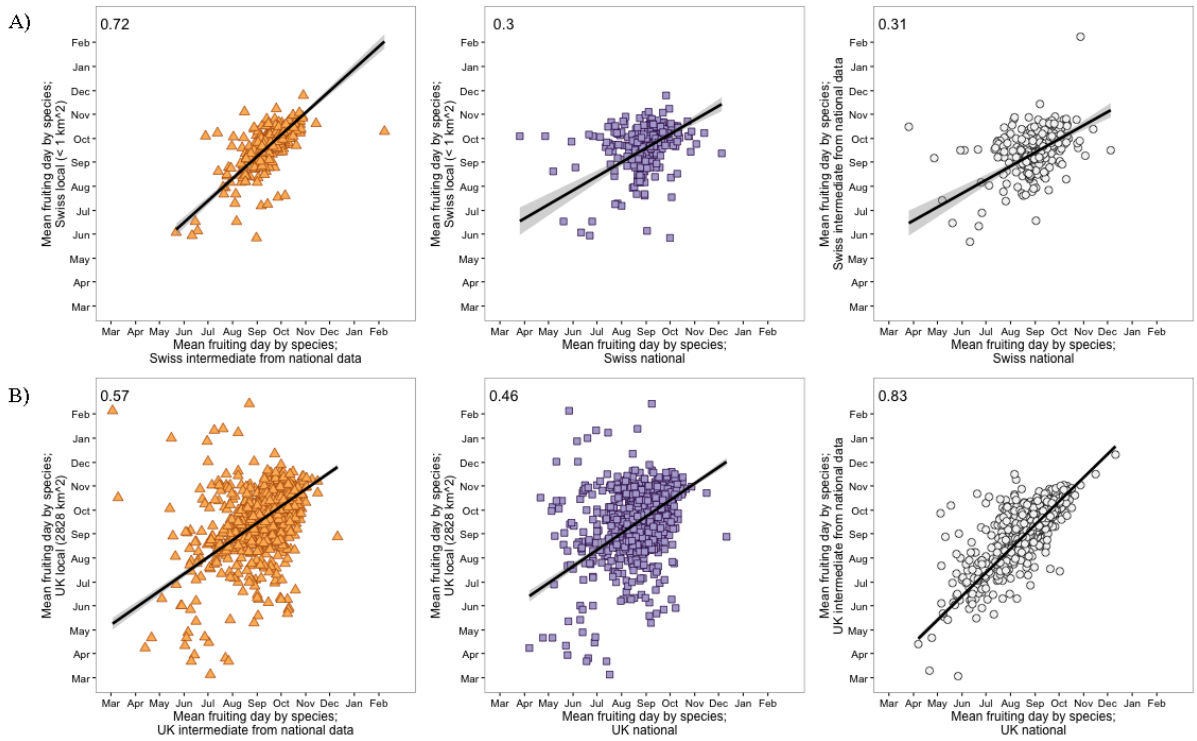
A)
0.72
Mean fruiting day by species; Swiss local (< 1 km^2)
Mean fruiting day by species; Swiss intermediate from national data
0.3
Mean fruiting day by species; Swiss local (< 1 km^2)
Mean fruiting day by species; Swiss national
0.31
Mean fruiting day by species; Swiss intermediate from national data
Mean fruiting day by species; Swiss national
B)
0.57
Mean fruiting day by species; UK local (2828 km^2)
Mean fruiting day by species; UK intermediate from national data
0.46
Mean fruiting day by species; UK local (2828 km^2)
Mean fruiting day by species; UK national
0.83
Mean fruiting day by species; UK intermediate from national data
Mean fruiting day by species; UK national
Feb Jan Dec Nov Oct Sep Aug Jul Jun May Apr Mar
Mar Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb

Figure 4

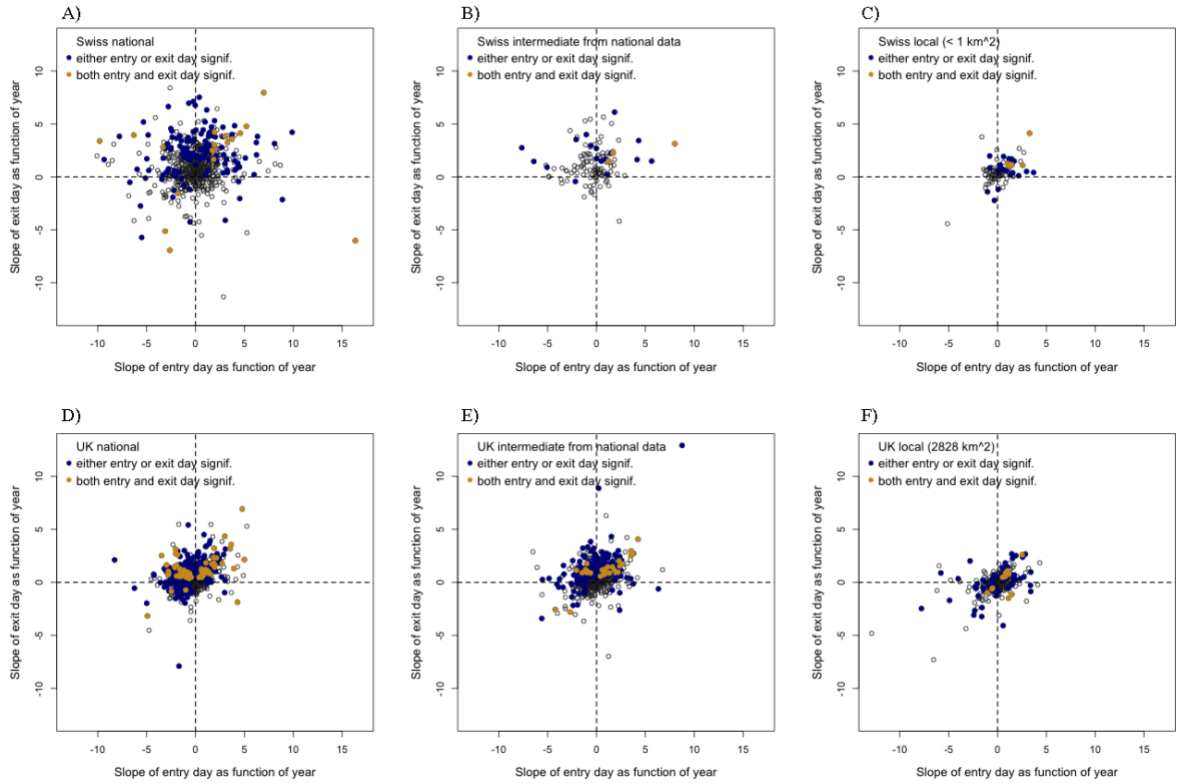
A)
Swiss national
either entry or exit day signif.
both entry and exit day signif.
B)
Swiss intermediate from national data
either entry or exit day signif.
both entry and exit day signif.
C)
Swiss local (< 1 km^2)
either entry or exit day signif.
both entry and exit day signif.
D)
UK national
either entry or exit day signif.
both entry and exit day signif.
E)
UK intermediate from national data
either entry or exit day signif.
both entry and exit day signif.
F)
UK local (2828 km^2)
either entry or exit day signif.
both entry and exit day signif.
Slope of exit day as function of year
Slope of entry day as function of year
-10
-5
0
5
10
15

Figure 5

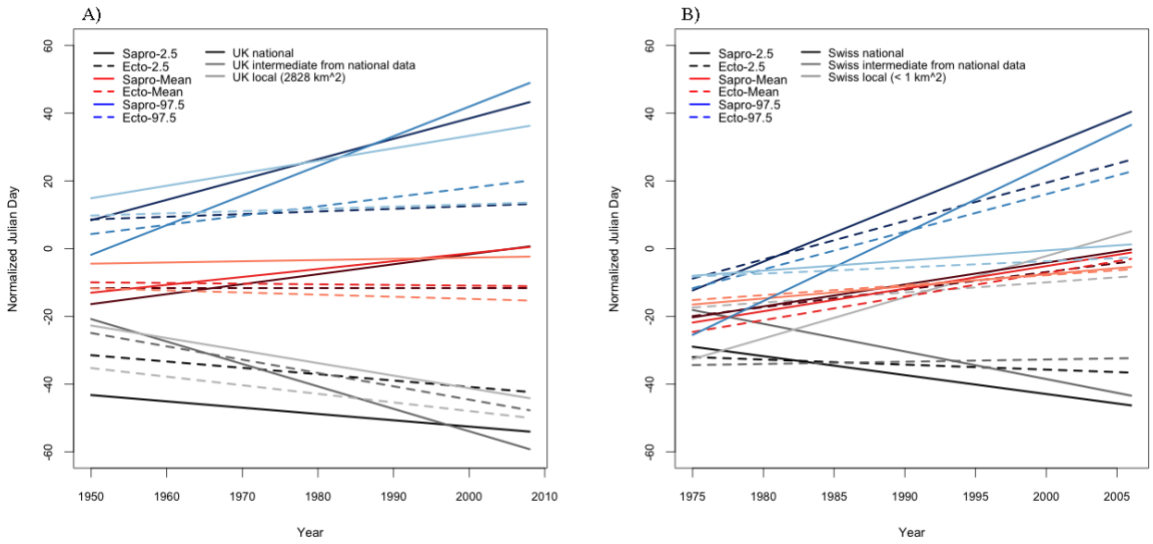
A)
Sapro-2.5
Ecto-2.5
Sapro-Mean
Ecto-Mean
Sapro-97.5
Ecto-97.5
UK national
UK intermediate from national data
UK local (2828 km^2)
Normalized Julian Day
Year
B)
Sapro-2.5
Ecto-2.5
Sapro-Mean
Ecto-Mean
Sapro-97.5
Ecto-97.5
Swiss national
Swiss intermediate from national data
Swiss local (< 1 km^2)
Normalized Julian Day
Year

Figure captions

Figure 1

Distribution of fruit body datasets used in the study. Two datasets, both national scale, were located in the UK and Switzerland. These data were analysed in their (A) entirety, as national scale data (light blue shading) as well as (B) intermediate scales (blue shading). Two datasets independent from the national scale data were available for each country (darker blue shading), the Gange data in the United Kingdom and La Chanéaz data in Switzerland. Data are entirely distributed across all ranges (see Andrew et al. 2017 for data point densities at the national scales).

Figure 2

Venn diagrams depicting the number of shared and unique species by dataset scale for the (A) Swiss (1975 - 2006) and (B) UK (1950 - 2008) data. Across the two scales, there were a total of 2,544 Swiss species and 2,861 UK species.

Figure 3

Phenology correlation plots of the mean ordinal fruiting days (start day = 01 March) by species. The three combinations by local, intermediate and national scale are provided for (A) Switzerland and (B) the UK. Note a species must be present in each scale to be included in this analysis. The larger scale of the comparisons is always plotted as the predictor value, on the x-axis, while the smaller scale is plotted as the response variable, on the y-axis. Each symbol represents a species. Each plot contains a linear regression (solid line) with a 95% confidence interval (shaded). Correlation coefficient values are provided in the upper left of each plot. For further statistics, refer to Supplementary material 2.

Figure 4

Shifts in fruiting season start and duration by species for each dataset scale during the periods 1975-2006 (Switzerland; A-C) and 1950-2008 (UK; D-F). Positive axis slope values reflect later entry or exit days in the season while negative reflect earlier entry or exit days, based on 97.5^{th} and 2.5^{th} percentiles, as a function of year and with varying sampling intensities accounted for. Filled in circles indicate species with statistically significant changes; dark blue either seasonal start or duration are significant while yellow are significant for both. Unfilled circles indicate species with non-statistically significant trends.

Figure 5

Overall annual trend shifts in the beginning, mean and end of the fruiting seasons for each dataset scale during the periods 1950-2008 (UK; A) and 1975-2006 (Switzerland; B). The analyses are averaged across all species and divided into nutritional modes (saprotrophic, solid lines, or ectomycorrhizal, dashed lines). Seasonal start is calculated by 2.5^{th} percentile (black to grey colours) and the end by the 97.5^{th} percentile (blue shades), along with the mean values (red shades). Dataset scales grade from local in lighter shades to national in darker shades, only demonstrated for one colour in the key. Sampling intensities were accounted for in the analyses with the expected trends at average intensities shown here.

Table captions

Table 1

Descriptive statistics of national and locally independent datasets, including subsets extracted to intermediate datasets. Data are from Switzerland and the United Kingdom.

	Switzerland			United Kingdom		
	national	intermediate (from national data)	local (La Chanéaz)	national	intermediate (from national data)	local (Gange)
Frequency of surveys	largely non-scheduled	--	weekly during growing season	largely non-scheduled	--	weekly; all sites covered per year
Area surveyed (km^2)	41285	ca. 12385	< 1	209331	--	2828
Type of collectors	opportunistic	--	research surveys	opportunistic	--	forays
Complete timescale available	1904 - 2014	1935 - 2014	1975 - 2006	1760 - 2014	1780 - 2014	1950 - 2008
Number of records	204135	63225	97358	895125	275637	41374
Number of species	2798	2105	332	2971	2437	1120
Equal timescale for analyses	1975 - 2006	1975 - 2006	1975 - 2006	1950 - 2008	1950 - 2008	1950 - 2008
Number of records	119009	32502	97358	773645	236781	41374
Percent of complete time scale: records	58.3	51.4	100.0	86.4	85.9	100.0
Number of species	2531	1838	332	2845	2307	1120
Percent of complete time scale: species	90.5	87.3	100.0	95.8	94.7	100.0

Table 2

The top fruiting fungal taxa (by per cent of total records) are provided for (a) the United Kingdom (1950 - 2008) and (b) Switzerland (1975 - 2006) across spatial scales. The top twenty most common taxa for each dataset (values in bold) in descending order (based on averages across all of the country datasets) to the least common. Note *Mycena metata* might be one example of an over-represented taxon at the local level; inference upon its abundance should be dealt with carefully.

a) United Kingdom

	national	intermediate (from national)	local (Gange)
Hypholoma fasciculare	**1.50**	**1.62**	**1.66**
Stereum hirsutum	**1.37**	**1.37**	**1.87**
Laccaria laccata	**1.15**	**0.98**	**1.25**
Russula ochroleuca	**0.98**	**1.00**	**1.16**
Pluteus cervinus	**0.89**	**0.98**	**0.99**
Amanita rubescens	**0.91**	**0.90**	0.69
Gymnopus dryophilus	**0.75**	**0.83**	**1.25**
Paxillus involutus	**0.96**	**0.80**	**0.83**
Mycena galericulata	**1.03**	**0.96**	**0.70**
Rhodocollybia butyracea	**0.78**	**0.79**	**0.98**
Lycoperdon perlatum	**0.82**	**0.78**	**1.06**
Mycena galopus	**0.88**	**0.72**	**0.92**
Laccaria amethystina	**0.65**	**0.75**	**0.91**
Coprinellus micaceus	**0.80**	**0.88**	**0.87**
Xerocomellus chrysenteron	**0.77**	**0.88**	0.61
Scleroderma citrinum	**0.70**	**0.71**	0.68
Phallus impudicus	**0.79**	**0.70**	0.64
Amanita citrina	0.53	0.68	0.29
Mycena pura	0.55	**0.68**	**0.80**
Clitocybe nebularis	0.61	**0.69**	**0.73**
Lycoperdon pyriforme	**0.77**	**0.82**	0.48
Armillaria mellea	0.56	0.59	**0.85**
Leccinum scabrum	0.54	0.60	0.36
Hymenopellis radicata	0.44	0.58	**0.88**
Amanita fulva	0.45	0.48	0.58
Lactarius quietus	0.61	0.51	0.40
Amanita muscaria	**0.66**	0.51	0.35
Imleria badia (*Boletus badius*)	0.50	0.54	0.35
Crepidotus variabilis	0.42	0.55	**0.70**
Boletus edulis	0.43	0.50	0.31
Cuphophyllus virgineus (*Hygrocybe virginea*)	**0.66**	0.39	0.31
Parasola plicatilis	0.39	0.27	**0.77**
Mycena metata	0.07	0.06	**1.10**

b) Switzerland

	national	intermediate (from national)	local (La Chanéaz)
Laccaria amethystina	**0.65**	**0.78**	**12.86**
Hypholoma fasciculare	**1.50**	**0.85**	**7.43**
Kuehneromyces mutabilis	0.32	**0.78**	**7.13**
Rhodocollybia butyracea	**0.78**	0.53	**6.42**
Russula ochroleuca	**0.98**	**0.67**	**5.90**
Armillaria ostoyae	0.07	0.15	**5.47**
Mycena pura	0.55	**0.71**	**3.28**
Xerocomellus chrysenteron	**0.77**	**0.83**	**2.54**
Cortinarius caperatus	0.03	0.32	**3.58**
Lactarius blennius	0.33	0.34	**2.97**
Russula nobilis	0.31	0.23	**3.01**
Stereum hirsutum	**1.37**	**1.00**	--
Laccaria laccata	**1.15**	**0.72**	**1.68**
Mycena galopus	**0.88**	**0.67**	**1.40**
Gymnopus dryophilus	**0.75**	0.39	**1.69**
Clitocybe gibba	0.32	0.33	**1.91**
Russula cyanoxantha	0.49	**0.98**	0.98
Cortinarius flexipes	0.10	0.28	**1.97**
Hygrophorus eburneus	0.06	0.31	**1.86**
Imleria badia (*Boletus badius*)	0.50	**1.02**	0.67
Russula fellea	0.32	0.32	**1.45**
Gymnopus confluens	0.42	0.38	**1.15**
Paxillus involutus	**0.96**	0.30	--
Amanita rubescens	**0.91**	**0.59**	0.19
Lycoperdon pyriforme	**0.77**	0.39	0.43
Phallus impudicus	**0.79**	0.23	--
Mycena galericulata	**1.03**	0.45	0.03
Entoloma rhodopolium	0.20	0.24	**1.08**
Lycoperdon perlatum	**0.82**	0.52	0.16
Lepista nuda	0.53	**0.91**	0.00
Pluteus cervinus	**0.89**	0.46	0.06
Marasmiellus ramealis	0.35	**0.57**	--
Lactarius camphoratus	0.17	**0.69**	0.49
Suillus grevillei	0.26	**0.72**	0.32
Coprinellus micaceus	**0.80**	0.33	0.08
Scleroderma citrinum	**0.70**	0.11	--
Tricholomopsis rutilans	0.42	**0.72**	0.02
Megacollybia platyphylla	0.27	**0.73**	0.16
Cuphophyllus virgineus (*Hygrocybe virginea*)	**0.66**	0.06	--
Amanita muscaria	**0.66**	0.24	0.06
Boletus subtomentosus	0.28	**0.64**	0.02
Mycena sanguinolenta	0.26	**0.57**	0.10