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LETTER

Temperature affects the timing and duration of fungal fruiting patterns across major terrestrial biomes

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Abstract

The Earth's ecosystems are affected by a complex interplay of biotic and abiotic factors. While global temperatures increase, associated changes in the fruiting behaviour of fungi remain unknown. Here, we analyse 6.1 million fungal fruit body (mushroom) records and show that the major terrestrial biomes exhibit similarities and differences in fruiting events. We observed one main fruiting peak in most years across all biomes. However, in boreal and temperate biomes, there was a substantial number of years with a second peak, indicating spring and autumn fruiting. Distinct fruiting peaks are spatially synchronized in boreal and temperate biomes, but less defined and longer in the humid tropics. The timing and duration of fungal fruiting were significantly related to temperature mean and variability. Temperature-dependent aboveground fungal fruiting behaviour, which is arguably also representative of belowground processes, suggests that the observed biome-specific differences in fungal phenology will change in space and time when global temperatures continue to increase.

KEYWORDS

biomes, climate change, fruiting behaviour, fruiting phenology, fungi, global

INTRODUCTION

Temperature and precipitation are primary drivers of many biological and ecological processes (Brown et al., 2004). Variations in temperature means and precipitation totals can affect species' distribution ranges (Chen et al., 2011), abundance rates (Chen et al., 2011) and the timing of life cycle events (Sherry et al., 2007). These climate-induced changes may also disrupt biotic interactions (Beard et al., 2019) and ecosystem processes (Cardinale et al., 2012) at different spatiotemporal scales. Fruit body (mushroom)-forming fungi are considered important for the functioning and productivity of all terrestrial ecosystems (Delgado-Baquerizo et al., 2020; Lustenhouwer et al., 2020; Peay et al., 2016; Semchenko et al., 2018). Symbiotic fungi supply water and nutrients to host plants (Kohler et al., 2015), decomposer fungi mineralise dead organic material, contributing to the global carbon cycle (Floudas et al., 2012; Peay et al., 2016) and both maintain complex food webs (Boddy & Jones, 2008). Fungal fruit bodies are the ephemeral reproductive structures in which spores are produced via complex reproductive modes (Billiard et al., 2011; Coelho et al., 2017). Altered fungal growth and fruiting conditions may diminish fungal phylogenetic (Bässler et al., 2022) and functional diversity (Bässler et al., 2021; Krah et al., 2019), biotic interaction (Crowther et al., 2015), plant drought resilience (Liu et al., 2022) and carbon sequestration (Clemmensen et al., 2013). Despite the many roles fungi play in terrestrial ecosystems, the sensitivity of their fruiting behaviour to climate remains unclear at large spatial scales (Boddy et al., 2014).

Here, we use 6.1 million fruit body records (Figure 1a) to understand fungal fruiting behaviour within and

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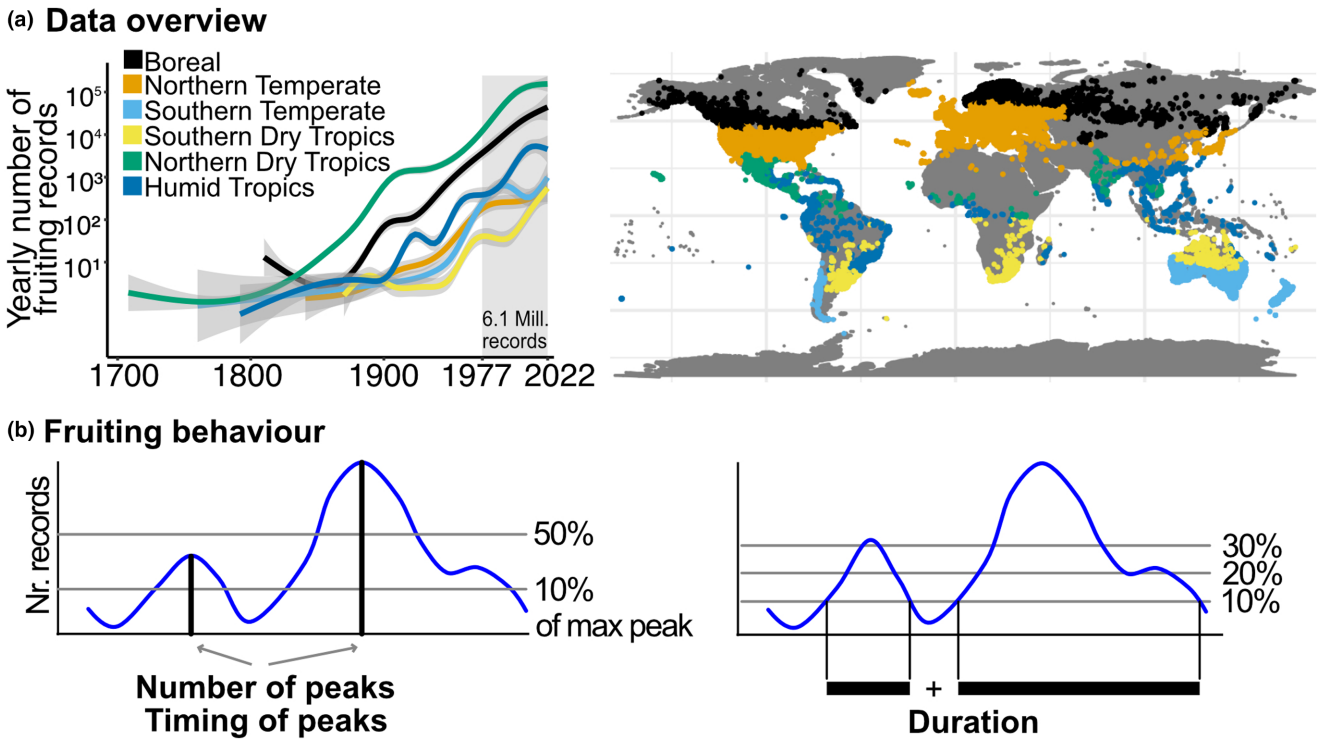

FIGURE 1 Global fungal fruiting records. (a) Data cleaning and standardization reduced the inventory from ca. 15 to 6.1 million records (grey bar indicates 95% of the data, falling between 1977 and 2022, for biome-specific number of records see Table S2. Global distribution of selected records. (b) Approach to estimate fruiting behaviour as the number of peaks, fruiting timing and fruiting duration. Lines indicate different thresholds when peaks or durations are counted. For further data processing and statistical analyses, see *Methods*.

among all major terrestrial biomes. More specifically, we explore the number of fruiting peaks, timing and duration (Figure 1b) across different climate types. In addition, we test the predictability of fruiting behaviour by temperature and precipitation variables. We finally explore whether fungi with different lifestyles, that is symbiotic and decomposer fungi, display similar or contrasting fruiting behaviour.

METHODS

Data processing

To address the global fruiting behaviour of fruit body-forming fungi, we first downloaded all records from the Global Biodiversity Information Facility (GBIF) (Gbif., 2017) with the query term 'Agaricomycetes'. Agaricomycetes is the largest fungal lineage with fruit bodies during their reproductive phase and ca. 21.000 species (Hibbett et al., 2014). This resulted in 14,877,200 records (17 January 2023, dataset doi: https://doi.org/10.15468/dl.wwr3yt). We then processed the data in the following way: (1) removal of all records without coordinate data (13,530,376 records left); (2) removal of records with a worse coordinate accuracy than 50 km (8,674,507 records left); (3) removal of flagged records based on the R package CoordinateCleaner, which was developed especially for GBIF data (Zizka et al., 2019). Using the function *clean_coordinates* with default tests, we removed, for example, records from urban areas and those that fell into water bodies (8,020,978 records left). Another source of error not handled by the CoordinateCleaner package are records where the calendar date is missing. In such cases, the first January of a given year is typically assigned. We thus deleted all records of this date (7,622,808 records left); (4) we removed species belonging to primarily nonannual genera (6,778,707 records left, for a genera-based assignment, see Table S1); (5) we visualized the number of records for the remaining time series and found a substantial increase in records over time and mainly since the mid-20th century (Figure 1a). To utilize most of the data and at the same time keep the time series rather short to avoid confounding effects due to environmental change over time, we used 95% of the data backwards, thus 1977–2022. Standardizing the data set to the years 1977–2022 led to the final dataset, which contained 6,152,849 records (Table S2). Although the dataset includes citizen science data, which may be prone to identification errors, it is important to emphasize that our approach does not rely on species identification.

Spatial grids and climate data

The smallest unit in our dataset is the grid-year within a biome. We assigned each record to a 1000 km × 1000 km

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grid cell across the globe, which we placed within the boundaries of biomes. This grid size reflects a balance between larger grids, which would overlap biome boundaries and smaller grids which would lead to a low grid-year number of records for some biomes. Note that species patterns in previous global-scale studies have been found highly consistent for 10 to 1000 km grid cells (Wolters et al., 2006) or 100 to 1000 km grid cells (Zuloaga et al., 2019). To define biomes, we used the biome classification from the global forest monitoring project (Hansen et al., 2010). This map includes the biomes: boreal, temperate, dry and humid tropics. The classification is based on the terrestrial ecoregions of the world (Olson et al., 2001). The humid tropics in this classification correspond to the tropical and subtropical moist broadleaf forests and are thus characterized by mainly warm and humid climates throughout the year; the dry tropics correspond to the tropical and subtropical grasslands, savannas and shrublands (Hansen et al., 2010; Olson et al., 2001), which was also termed as 'arid' (Cui et al., 2021). We added the biome information using the R package sp based on the centroids of the grids (Pebesma & Bivand, 2005). Since grids were placed within the boundaries of biomes, some grids contained only an island but no other land mass. In such cases, the grid centroid was situated within the ocean and thus the biome could not be extracted. For such grids, we assigned the nearest neighbouring biome. Due to the summer–winter time difference between hemispheres, we further split some biomes into a northern and a southern hemisphere. We split the temperate biome into 'Northern temperate' and 'Southern temperate' and the dry tropics into 'Northern dry tropics' and 'Southern dry tropics'. The boreal zone is only present in the northern hemisphere. The humid tropics occur near the equator, and thus, the seasons do not substantially differ between the northern and southern hemispheres. We plotted each record according to its biome on the world map (Figure 1a).

We added climatic variables to our gridded dataset. We used the climate research unit (CRU) TS Version 4.06 (Harris et al., 2020) and retrieved the monthly temperature mean and precipitation sum for each grid-year between 1977 and 2021. Since the dataset did not contain 2022, we used the mean values based on the last ten years (2012–2021) and assigned them to 2022. Based on this monthly grid-year climate dataset, we calculated for each grid-year measures of mean and variability: the average temperature mean and precipitation sum and their standard deviations.

Weekly fruiting data and fruiting behaviour splines

To gain a basis to calculate fruiting behaviour, we estimated fruiting curves for each grid-year using general additive models (GAMs). Prior to the GAMs, we (i) removed grid-years with less than 50 records; (ii) summed the number of records on a weekly basis for each grid-year. Note that the number of records differed substantially across grid-years. We are aware that 50 records per grid-year at the grain size of our study can cause biases. We addressed this issue statistically and by exploring thoroughly the raw data (see sensitivity analyses in the next paragraphs).

We fitted separate GAMs for each grid-year for all fungi and each lifestyle separately (see below '*Lifestyles*') using the function *gam* from the R package mgcv (Wood, 2011). Each GAM had the number of records as the response variable and the week as a predictor. Since seasonal data across years should show a cyclic pattern, we estimated a cyclic cubic spline. Furthermore, since the number of records also contains zeros, we used a binomial error term with loglink function. We further did not specify the number of outer knots (k = −1) and used restricted maximum likelihood estimation (REML), which is more robust (conservative) with smaller datasets. The GAM was specified as 'gam(nr_records ~ s(week, bs = 'cc', k=-1), family=nb(link='log'), method='REML')'. Although this worked well in most cases, this model failed to converge in 3% of grid-years. In these cases, we used a less conservative model specification using maximum likelihood estimation (ML) and removed the negative binomial error term and retained the family specification and cyclic model term. This led to convergent and, visually, good fits to the raw data in most cases. Finally, we visually compared all GAM cyclic cubic splines with the raw data and deleted 5% grid-years with poor fits (e.g., horizontal linear fits where data are scarce). For the grid-year-based splines, see Figure S1.

We performed a sensitivity analysis to determine the number of records that allow robust estimation of the fruiting cyclic cubic splines. For each biome, we used the grid-year with the highest record count and down-sampled the number of records to 50, 60, 80, 100, 120, 140 and 160 records. For each of these thresholds, we repeated the random sampling 100 times. We then compared the splines (predicted fits) based on the full dataset to the splines based on down-sampled datasets. We used Pearson's correlation coefficient r between full and down-sampled splines and compared the peak timing based on visual inspection. For the boreal and temperate biomes, we found $r > 0.8$ for a down-sampling to 50 records, and for the dry and humid tropics for a down-sampling to 120 records (not shown). However, in the dry and humid tropics, the peak timing was largely consistent already for a down-sampling to 50 records. We thus used at least 50 and 120 records per grid-year for our analyses and found consistent results. Therefore, we display results for the 50-record threshold.

Another sensitivity exploration concerns the chosen time interval (1977–2022), which falls within the climate change era (Mann et al., 2004). To address this issue, we first considered temporal uncertainties in the data

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while focusing on the spatial pattern among and within biomes which is the main focus of the study (see *Data visualization and statistical analysis*). Second, to illuminate whether earlier and later subsets of the full dataset show a consistent pattern, we show fruiting splines for 1977–2000 and 2001–2022 and found a consistent pattern (Figure S2). This exercise addressed both the temporal effects of climate warming and the effects of sampling bias. Please note that temporal changes in fruiting behaviour caused by climate change are not the focus of our analyses due to data constraints.

Fruiting behaviour variables

We generated comparable fruiting behaviour splines for each grid-year to determine fruiting behaviour measures. Since the absolute number of records may differ on average between grid-years, we scaled the splines between 0 and 1. Based on each grid-year cyclic cubic fruiting spline, we quantify three variables (Figure 1b): (i) the number of peaks, (ii) the timing of each fruiting peak (week of maximal fruiting) and (iii) the total duration of fruiting (above a threshold, e.g., 10%, see below). The variables are frequently used to characterize phenology (Boyce et al., 2017; Feng et al., 2013). The number of peaks and timing was counted for each maximum (R package ggpmisc), above a threshold. We used 10% and 50% as thresholds (Figure 1b). The 10% threshold is intended to provide an upper estimate of the number of peaks. Using the 50% threshold, peaks below 50% of the maximal peaks are not counted, thereby providing a lower estimate of the number of peaks. Following the method of White et al. (1997), we defined fruiting duration as the total number of weeks during which the value of the fitted spline was above a certain threshold. We chose to use thresholds to quantify duration (Figure 1b) higher than 0% to capture main fruiting events rather than outlier fruiting of species that are able to fruit at extreme conditions (e.g., *Flammulina velutipes* in the winter in boreal and northern temperate biomes). After visual inspection of the fruiting splines, we chose 10%, 20% and 30% to capture an upper, medium and lower estimate of duration.

Data visualization and statistical analysis

We were interested in the spatial variability of the fruiting behaviour measures within and among biomes and how they are related to climate. Therefore, we (1) showed the raw data of the number of peaks, timing and duration across biomes, (2) showed their spatial variability together with temporal uncertainty (error bars) in the data and (3) modelled the response of fruiting behaviour with climatic mean and variability. For (1), we showed density distributions for each fruiting behaviour variable across biomes and for the thresholds. For (2), we first calculated the standard deviation of each of the three fruiting behaviour variables within each year, as a measure of spatial variability. If peak timing is near the beginning or end of the calendar year, standard deviations of timing may be overestimated. The cases were few, with 3% of grids' peak timing falling into weeks above 47 and below 5. To address this problem, we rotated weeks of peak timing (52 times increment by 1; when 52 is reached restart from 1) and recalculated the standard deviation and chose the minimum standard deviation estimate. Then, we calculated the mean spatial variability across the years. To gain a measure of temporal uncertainty, we generated 1000 nonparametric bootstraps and obtained the 95% confidence limits for the observed population mean without assuming normality (R package Hmisc, (Harrell Jr & Many others, 2017)). Using the coefficient of variation (CV) instead of the standard deviation produced consistent results. Furthermore, we downsampled the temperate and boreal biomes to sample sizes observed for the less sampled biomes (i.e., tropics) and compared the mean variability. This exercise produced robust and consistent results, where the mean of repeated downsampling was tightly distributed around the mean of the full analysis (not shown). For (3), we used GAMs to model the response of the number of peaks and duration to temperature and precipitation mean and variability. We decided to use univariate models (separate models for each predictor) and a comparison among predictors based on the effect sizes and R^2's due to co-linearity among predictors leading to spurious statistical inferences. Therefore, we Bonferroni adjusted the *p*-values. Note that using timing (week-position) as a response is not straightforward and interpretable, and thus, we instead used the monthly number of records per grid-year in relation to monthly climate variables. Climate data at a global scale were available at a monthly resolution (CRU data). For each response, we fitted one overall GAM (cross-biome) and GAMs separately for each biome to retrieve goodness-of-fit (R^2) for each biome. For the number of peaks as a response, we specified the GAM as: 'gamm(nr_peaks ~ s(grid-year climate variable, k=-1), family=poisson(link='log'), random=list(grid=~1))'; for the fruiting duration as: 'gam(duration ~ s(climate variable, k=-1), random=list(grid=~1))'; for timing, we first removed grid-years with less than 100 records and month with less than 10 records and specified: 'gam(log10(nr_rec) ~ s(monthly grid-year climate variable, k=-1), random=list(grid=~1, year =~1))'. We added a random effect on grid for the number of peaks and duration because years are replicated in grids. For timing, we $\log_{10}$-transformed the number of records and used grid and year as random effects because months were replicated in years and grids. For the number of peaks and duration models, we used four climate variables: temperature mean, precipitation sum, temperature variability (SD) and precipitation variability (SD). Standard deviations represent the variation of the mean temperature and precipitation sums across the months for each grid-year. For the timing (number of records) models

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based on monthly data, we used two climate variables: monthly temperature means and monthly precipitation sums. In the case of timing, we used the monthly number of fruiting records and thus we did not include within-year climate variability. The precipitation sums and variability values both showed left-skewed distributions and thus were $\log_{10}$-transformed prior to analyses.

Lifestyles

We focused on an overall fungi analysis. However, since there are two primary lifestyles within Agaricomycetes, we repeated our analyses for decomposers (saprotrophic fungi) and symbionts (ectomycorrhizal fungi). To attribute each observation to a lifestyle, we used the most recently available lifestyle classification (Põlme et al., 2020). This fungal trait database contains two lifestyle assignments for each genus, the 'primary_lifestyle' and the 'secondary_lifestyle'. The primary lifestyle describes the predominant lifestyle within a genus, the secondary is the second most abundant lifestyle within a genus. For both, we recoded dung, litter, wood and soil saprotrophs to 'decomposer' and ectomycorrhizal to 'symbionts'. Within the secondary lifestyle, we further classified unspecific_symbiotroph to 'symbionts'. We deleted mycoparasites and plant_pathogens. Furthermore, root-associated and bryophilous fungi are not clearly assignable to decomposers or symbionts. We tried both, which resulted in a consistent pattern. We here placed them in symbionts for further analyses. We further denote the primary lifestyle coding as 'decomposer' and 'symbionts' and the secondary lifestyle coding as 'decomposer2' and 'symbionts2'. The dataset is balanced between the lifestyles with 2,557,882 symbiotic and 3,594,967 decomposer fungal records. Note that we classified the lifestyle based on the genus level, which might introduce errors and uncertainty if genera are misidentified. We assume that identification errors on a genus basis should be relatively small. To quantify the potential error by misidentification on the genus level, we randomly drew 100 records with images. We found only one image, which was wrongly identified.

RESULTS

The barplot of the fruiting behaviour 'number of peaks' showed most frequently one fruiting peak per grid-year within and among biomes (Figure 2). We found clear fruiting timings in boreal, temperate and northern dry tropics and rather broad and flat timings for southern dry and humid tropics (Figure 2). For boreal and northern temperate biomes, peaks of grid-years which showed one peak fell into fall (ca. weeks 35–45) and peaks of grid-years with two peaks fell into fall and spring (ca. weeks 15–25; Figure 2). For the duration, we found a wide range of fruiting durations in boreal, the temperate and the northern dry tropics and more distinct and longer durations in the southern dry and humid tropics (Figure 2). There was some variability within biomes considering the three thresholds (10%, 20% and 30%), and consistent pattern among biomes.

The spatial variability of the number of peaks was low across biomes (Figure 3). The 10% threshold showed an overall trend towards higher variability across biomes than the 50% threshold (Figure 3). For the grid-years with one peak, we found a trend towards lower mean spatial variability in fruiting timing in boreal, the temperate and the northern dry tropics compared with the southern dry and humid tropics (Figure 3). For the second peak, we found only little differences between biomes, but the humid tropics showed a trend towards higher variability than the other biomes (Figure 3). We found a trend towards higher spatial variability in fruiting duration in boreal and northern temperate biomes than the dry and humid tropics (Figure 3). The southern temperate biomes showed an intermediate duration variability (Figure 3).

In response to climate variables across biomes, the number of peaks showed linear but nonsignificant effects (Figure 4; Table S3), whereas we found significant responses of timing and duration (Figures 5 and 6; Tables S4 and S5). Fruiting timing (i.e., the number of monthly records) was significantly related to monthly temperature and monthly precipitation across biomes (Figure 5; Table S4). Fruiting timing showed a saturating increase for monthly temperature and a sigmoid to almost linear increase for monthly precipitation. Fruiting duration was significantly related to temperature mean, showing a saturating increase, with temperature variability, showing a decrease, and with precipitation sums, showing a positive trend (Figure 6; Table S5).

Within biomes, we found overall low predictability of the number of peaks (Table S3), and high predictability for timing and duration in some cases (Tables S4 and S5). Within each biome, fruiting timing was significantly related to temperature mean and variability (Figure 5; Table S4). Fruiting durations in the boreal and northern temperate biomes were significantly related to temperature mean and variability (Figure 6; Table S5). The southern temperate and northern dry tropical fruiting duration were significantly related to precipitation mean (Figure 6; Table S5). The southern dry tropical fruiting duration was significantly related to the temperature mean (Figure 6; Table S5, significant for the 10% and 20% threshold). The humid tropical fruiting duration showed no significant effects with climatic variables (Figure 6; Table S5).

For the lifestyle-based analyses, we found mostly consistent results with the full analyses (Figures S3–S6; Tables S6–S8), but also some differences. We found slightly more constrained timing and shorter duration of the main fruiting peak for symbionts than decomposers in boreal and northern temperate biomes (Figures S3

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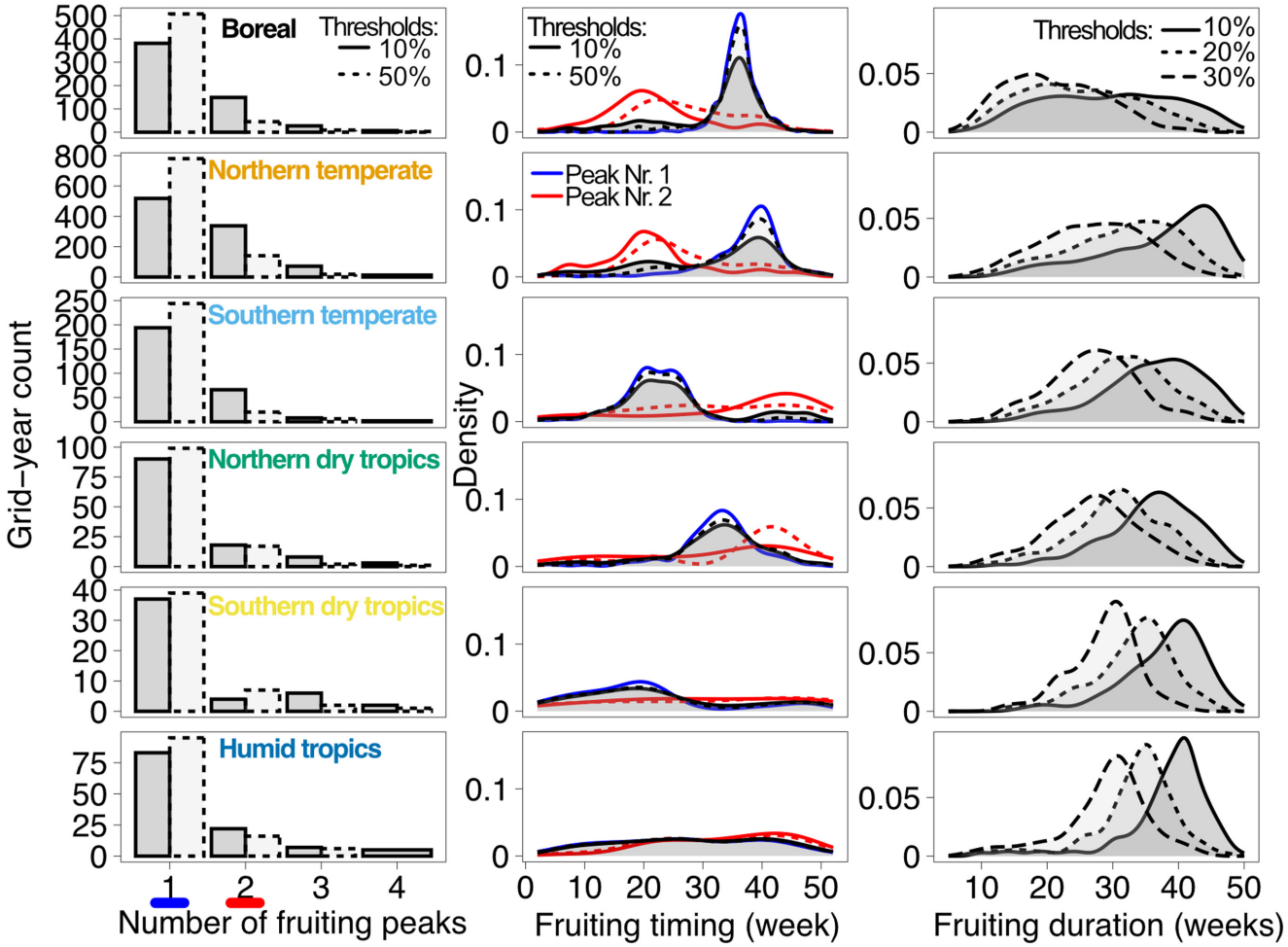

FIGURE 2 Distribution of fruiting behaviour measures based on grid-years. For the number of peaks and timing, we used two thresholds, namely 10% and 50%, meaning only peaks were included which were above 10% or 50% of the maximum peak. For the duration, we used three thresholds, namely 10%, 20% and 30%, meaning weeks were considered at the respective thresholds of the maximum peak (for the thresholds see Figure 1b). For the number of peaks, the number denotes the count of peaks found in the grid-years. We then separated the timing for grid-years with one peak (Peak Nr. 1) and grid-years with two peaks (Peak Nr. 2). For Peak Nr. 2, the larger peak largely overlapped with the curve for Peak Nr. 1 and is therefore not visible.

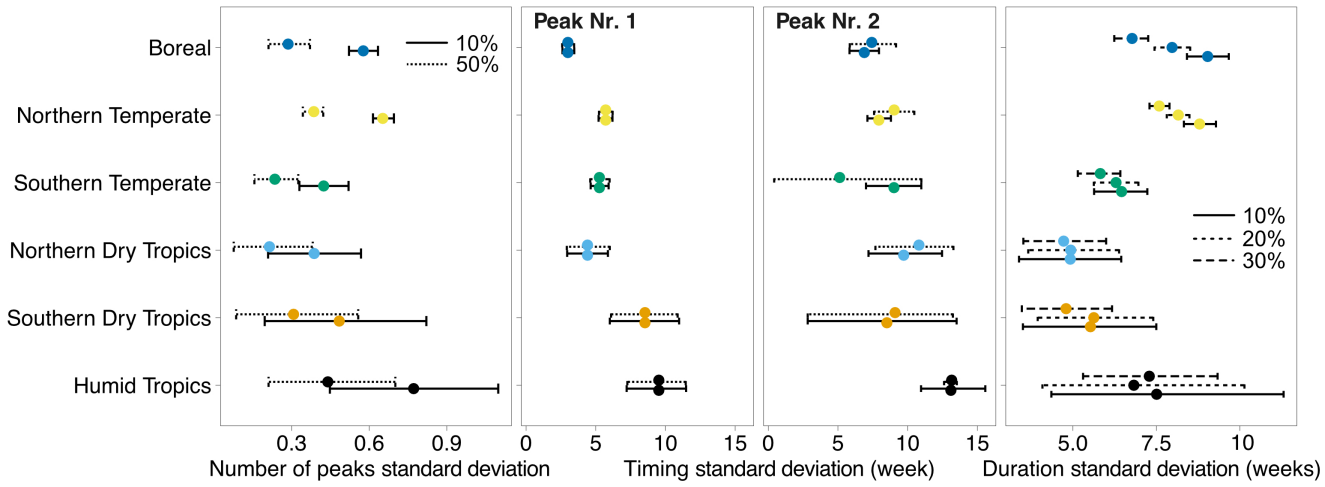

FIGURE 3 Variability of fruiting behaviour values among and within biomes. Points are mean variabilities and error bars based on 1000 bootstraps and error bars indicate the 95% confidence interval of the temporal uncertainty in the data. For the number of peaks and timing, we used two thresholds, namely 10% and 50%, meaning only side-peaks were included which were above 10% or 50% of the maximum peak. For the duration, we use three thresholds, namely 10%, 20% and 30%, meaning weeks were considered at the respective thresholds of the maximum peak.

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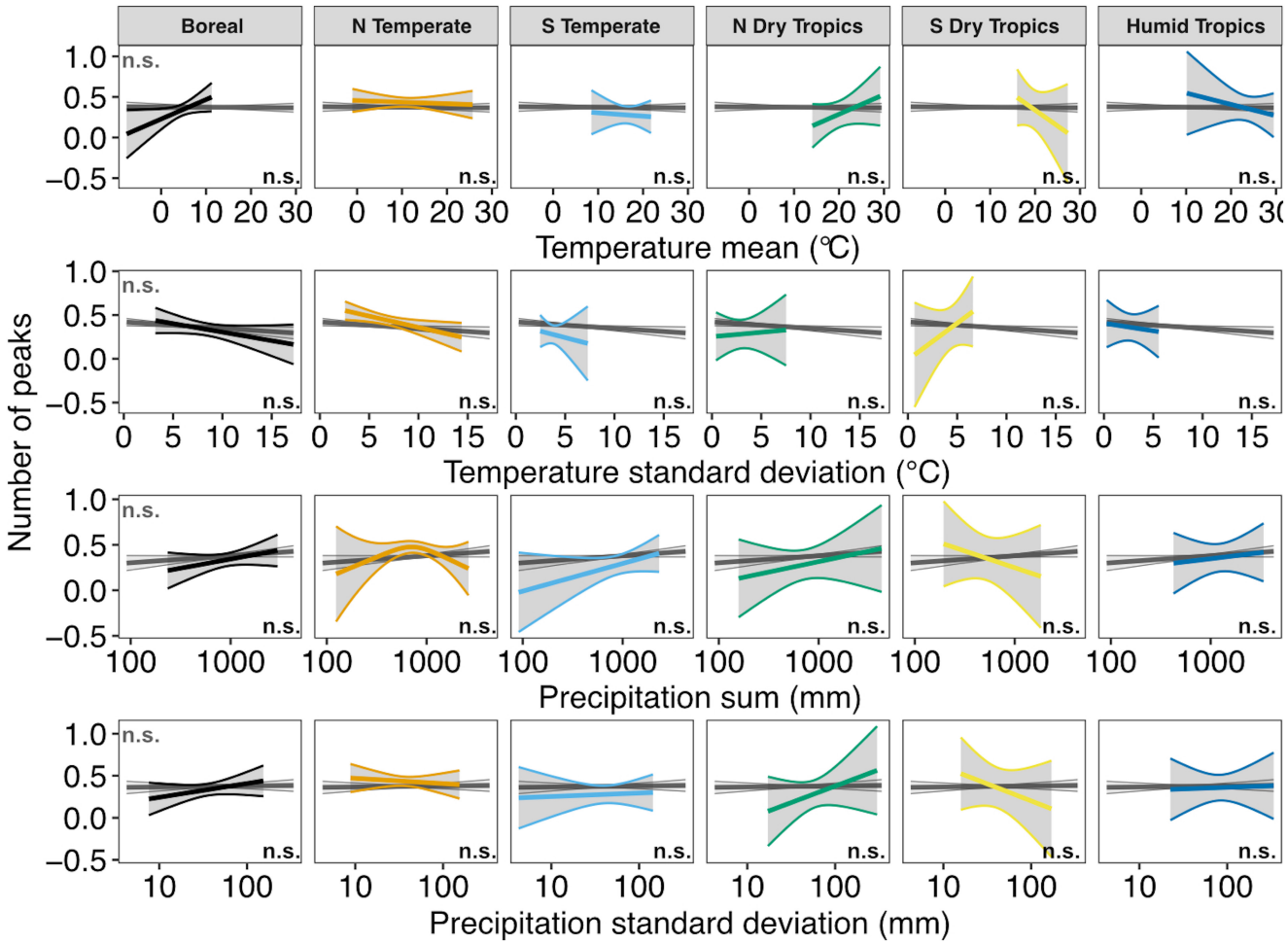

FIGURE 4 Fruiting number of peaks in relation to temperature and precipitation mean and variability. Shown are the results for the 10% threshold (see Figure 1b). Fits are based on univariate general additive models. We show the standard errors as a confidence interval. Note that precipitation was $\log_{10}$-transformed. N = Northern; S = Southern; sig. = significant at an alpha level of 0.0125 (Bonferroni-adjusted); n.s. = nonsignificant. Grey significance labels are for the cross-biome fits, and significance is given at the top-left of the leftmost panel; black significance labels are for the respective biome. For full statistics, see Table S3.

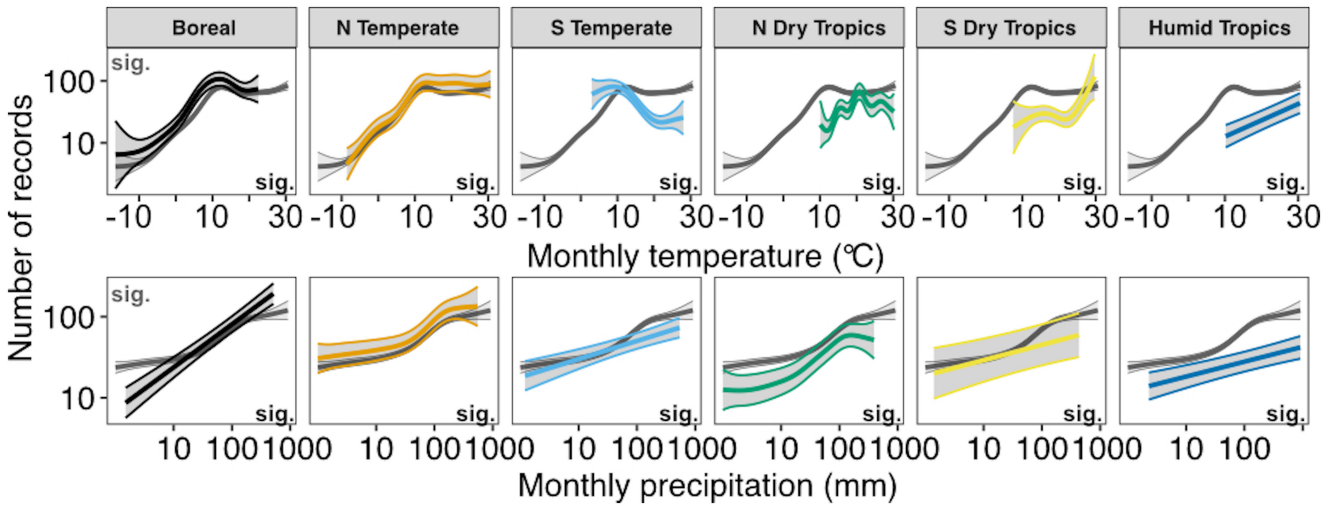

FIGURE 5 Fruiting timing (number of records) in relation to temperature and precipitation mean and variability. Fits are based on univariate general additive models. We show the standard errors as a confidence interval. Note that precipitation and the number of records values were $\log_{10}$-transformed. N = Northern; S = Southern; sig. = significant at an alpha level of 0.025 (Bonferroni-adjusted); n.s. = nonsignificant. Grey significance labels are for the cross-biome fits and significance is given at the top-left of the leftmost panel; black significance labels are for the respective biome. For full statistics, see Table S4.

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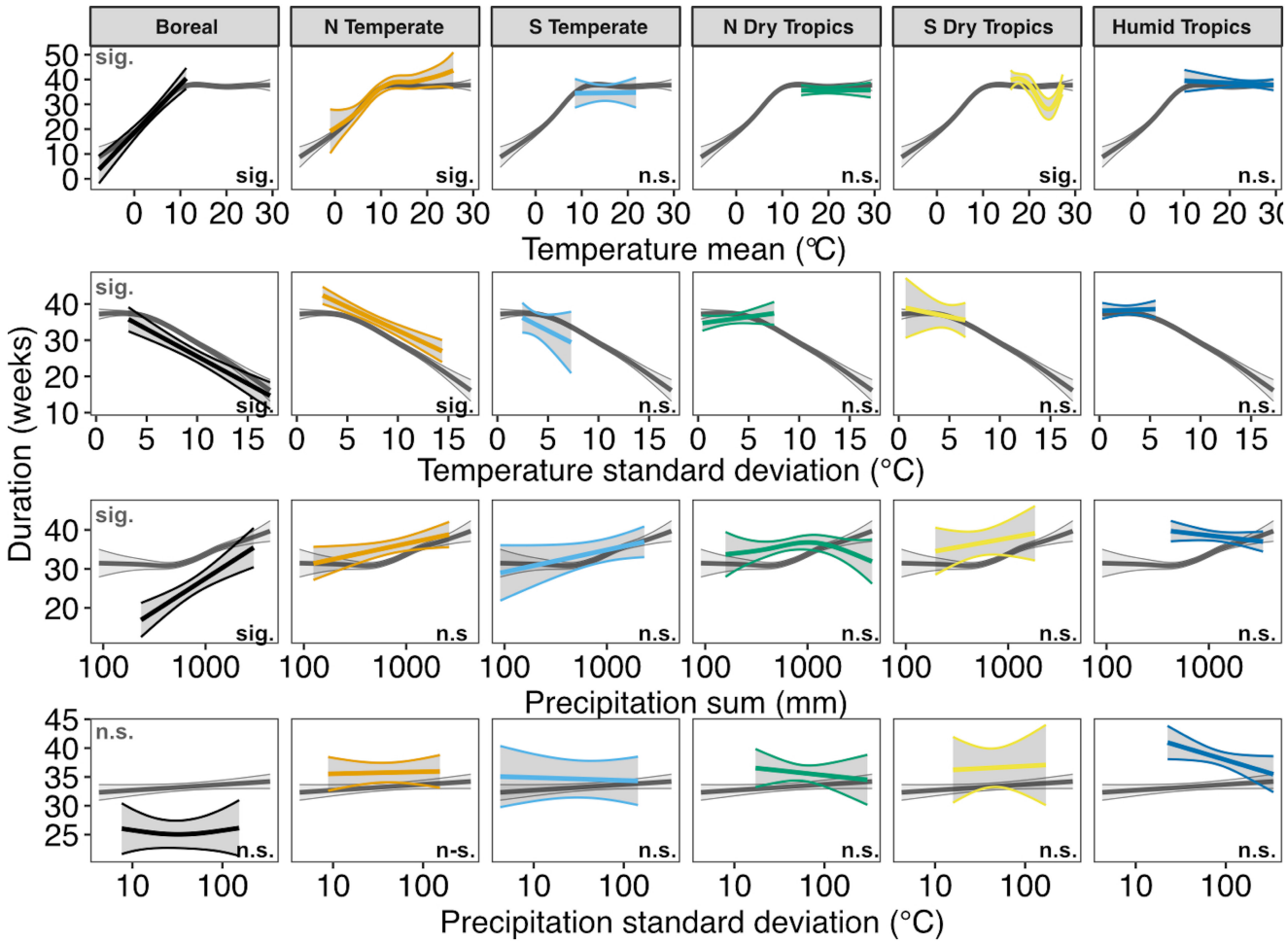

FIGURE 6 Fruiting duration in relation to temperature and precipitation mean and variability. Fits are based on univariate general additive models. We show the standard errors as a confidence interval. Note that precipitation and the number of records values were $\log_{10}$-transformed. N = Northern; S = Southern; sig. = significant at an alpha level of 0.0125 (Bonferroni-adjusted); n.s. = nonsignificant. Grey significance labels are for the cross-biome fits and significance is given at the top-left of the leftmost panel; black significance labels for the respective biome. For full statistics see Table S5.

and S4). Furthermore, symbiotic fungal fruiting duration showed higher R^2s with temperature mean and variability within boreal and northern temperate biomes (Table S8).

DISCUSSION

Our first global assessment of fungal fruiting behaviour revealed the following key insights: (i) most frequently one fruiting peak per grid-year in all biomes; (ii) biomes differed substantially in fruiting timing pattern with a strong spatial variability in southern dry and humid tropics, while in other biomes, particularly the boreal and temperate biomes, the timing was more coordinated within a year across grids; (iii) spatial variability of fruiting duration was more pronounced in boreal and northern temperate biomes; (iv) temperature explained fruiting behaviour better than precipitation; (v) fruiting timing and duration were more strongly related to temperature than the number of peaks; and (vi) fruiting behaviour patterns were mostly similar for decomposer and symbiotic fungi.

One main fruiting peak in most years across biomes

Local studies from the northern hemisphere showed that the fruiting optima within a year are related to specific weather conditions (Boddy et al., 2014). For example, Straatsma et al. (2001) showed that fungal productivity and appearance causing a fruiting peak are correlated with specific temperature and precipitation conditions within a year. From these studies, we might expect that the temporal fruiting optima within a year are related to one suitable window of opportunity driven by external factors (e.g., weather conditions and resource availability). However, one might assume that the number of windows of opportunity differs among biomes. Opportunity

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constraints, caused, for example by unfavourable weather conditions, seem more prevalent in climate seasonal biomes like the boreal or temperate biomes than in the humid tropics. Therefore, for the humid tropics, one might expect more than one fruiting peak within a year, as it was found in the flowering and fruiting phenology of tropical plant species (Numata et al., 2022). However, according to our data, most grid-years of the major biomes showed one fruiting peak (Figures 2; Figure S1). This indicates that even though variability of external factors like weather conditions and hence windows of opportunities differ among biomes, there are similar temporal within-year fruiting cues in all biomes. These cues might be caused by climate and weather conditions (Sakamoto, 2018) and other factors like resource availability (Boddy et al., 2014) or co-evolution with the phenology of co-occurring species such as dispersal vectors (Oliveira et al., 2015). Furthermore, we found grid-years with two peaks in all biomes, which was more pronounced for temperate and boreal biomes. This may be explained by early fruiters in spring (Boddy et al., 2014). The secondary peak indicates that species differ in their fruiting strategies and that different factors exist that serve as fruiting cues (Sakamoto, 2018). Variable strategies are observed in plants for flowering and fruiting phenology (Numata et al., 2022) in humid tropics and can also be assumed for fungi; however, empirical evidence is scarce (Boddy et al., 2014). Studies for fungal fruiting phenology are scarce, particularly in the humid tropics, which is also the case in plant science (Davis et al., 2022). However, one local study from humid tropical China found no notable fruiting peaks but focused only on the main rainy fruiting season (Li et al., 2018). More studies at different spatial scales are therefore needed, focusing on the mechanistic link between within-year fruiting peaks and the underlying factors across biomes.

Spatially variable versus spatially coordinated timing of fruiting

We found spatially more coordinated fruiting in boreal and temperate biomes compared to humid tropics (Figures 2 and 3). One explanation might be that low and freezing winter temperatures in boreal and parts of the temperate biome constrain fungal growth (Dix & Webster, 2012) and thus the timing of fruiting across large spatial scales. Furthermore, the high consistency in fruiting timing in boreal and temperate biomes is likely explained by the severe temperature drop in fall as a universal fruiting cue (Sakamoto, 2018). However, the temperature drop does not explain the secondary peak in spring for the boreal and northern temperate biome. In contrast, the humid tropical biome is characterized by generally homogenous within-year temperature conditions, high precipitation totals and low levels of precipitation seasonality (Walter, 2012). Therefore, periods which prohibit major fungal growth are not present in humid tropics that could severely constrain fruiting. Furthermore, in the humid tropics, a coordinated fruiting cue is likely absent. One explanation for the high spatial timing variably in the humid tropics might be that the rainy season timing differs strongly among areas of humid tropics and within an area in time (McGregor & Nieuwolt, 1998). Alternatively, it might be a set of different fruiting cues that result in the heterogeneous spatial fruiting pattern across the humid tropical biome (Figure S1). Which fruiting cues cause the timing of fruiting in a given locality (grid), causing the observed spatial variability across the tropics must be left to future studies.

Higher spatial variability of duration in northern biomes compared to tropics

The spatial variability in fruiting duration is more pronounced in boreal and northern temperate compared with the other biomes (Figure 3). Variability in fruiting duration across grids in these biomes indicates locality-specific fruiting duration constraints in a given year. Previous studies from boreal and temperate Europe showed that fruiting duration change is correlated with climate variables (Boddy et al., 2014; Büntgen et al., 2012; Kauserud et al., 2008). This implies that the observed spatial variability in boreal and temperate biomes is caused by specific climate conditions in a year, favouring or limiting fruiting duration (e.g., temperature and moisture conditions). Such kinds of constraints seem not relevant in tropical biomes which showed more consistent fruiting duration patterns across space.

Importance of temperature for fungal behaviour and climate change implications

Among our fruiting behaviour measures, duration showed the strongest response based on effect sizes and R^2's to climate and especially to temperature mean and variability. With increasing temperature, fruiting duration increased and at high mean temperatures reached saturation (Figure 6). This indicates that the effect of increasing warming is biome-dependent. Previous studies showed that in European boreal and temperate biomes, fruiting duration has, on average, extended (Boddy et al., 2014; Gange et al., 2007; Kauserud et al., 2008). Based on our dataset, we found an increase and then saturation in duration within the northern temperate biome (Figure 6). Thus, in areas with low mean annual temperatures fungal communities will likely increase in total fruiting duration with climate warming. For example, in boreal and temperate biomes climate constraints might decrease with climate warming and thus prolong fruiting opportunities (Cleveland et al., 2011). In contrast, in

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areas with intermediate and warm mean annual temperatures (e.g., humid tropics), fungal fruiting responses to climate warming might be limited as fruiting opportunities are not constrained by temperature.

In the boreal biome, we thus would also predict an increase in duration for most areas. Furthermore, although timing showed low R^2's in our climate models, the response is very similar to duration with an increase and saturation with mean annual temperature. Thus, the potential of a change in timing with climate change might also be very location-specific. Whether this might lead to phenological mismatches with other organisms is unclear and deserves further attention.

We further observed a negative relationship between fruiting duration and temperature variability within a year across biomes. Hence, strong temperature variability in a year and locality can limit fruiting duration. For example, strong temperature variability in boreal and temperate biomes reflects unfavourable fruiting conditions (e.g., long winter freezing). It has been suggested that with increasing temperatures in winter, seasonality will diminish in cold regions of the northern hemisphere (Xu et al., 2013). Therefore, fruiting duration might increase with global warming in boreal and temperate biomes and currently available studies suggest this scenario (Boddy et al., 2014). In tropical biomes, low-temperature variability is related to higher fruiting durations. Climate models predict increasing temperature variability in tropical biomes (Bathiany et al., 2018). Hence, potential shifts from an aseasonal to a seasonal pattern may critically change fungal fruiting behaviour in tropical biomes.

Fruiting behaviour of different fungal lifestyles

Besides favourable climatic conditions (Boddy et al., 2014), successful resource acquisition is required for fruiting. Prior to fruiting, a storage mycelium needs to be built, from which carbohydrates are allocated towards the mushroom (Kües & Liu, 2000). It has been suggested that the fruiting of symbionts can only occur in a narrow time interval, restricted by the main photosynthetic activity of the host plant and, therefore, carbohydrate allocation to the fungus (Boddy et al., 2014; Brown et al., 2022; Sato et al., 2012). Consistent with these results, we found a pattern of more coordinated and shorter fruiting for symbiotic fungi compared with decomposers in boreal and temperate biomes. Furthermore, symbiotic fungi showed a weaker spring fruiting peak compared with decomposer fungi (Figure S4), suggesting that they require photoassimilates that are mainly available later in the season. However, other studies found no difference in fruiting patterns between lifestyles, especially in the tropics (Li et al., 2018; Tuno et al., 2020), where we also found only minute differences. Although lifestyles showed some gradual differences in the boreal and northern temperate biomes, overall, we found similar fruiting behaviour patterns across biomes. One explanation might be that fruiting is more strongly driven by external environmental factors for fungi (Sakamoto, 2018), rather than the resource acquisition strategy. The slightly more constrained fruiting in symbiotic fungi in boreal and northern temperate biomes might be due to the host constraining fruiting of symbiotic fungi or due to a narrower climatic tolerance of symbiotic fungi compared with decomposers.

Cautionary notes

Besides important insights, our dataset contains limitations. (1) Community science data typically contain errors. However, we used an established cleaning procedure and additional cleaning steps, which excluded 60% of the records. (2) The resulting dataset displays an imbalance in the number of records between biomes (both spatially and temporally). To gain meaningful fruiting splines per grid-year, we applied data cut-offs and visually inspected each cyclic cubic spline and excluded it if it showed extreme over- or underfitting to the raw data. Furthermore, we applied down-sampling approaches and different thresholds for our fruiting behaviour variables to display remaining uncertainty. (3) We conducted analyses based on fruiting records and not based on species numbers. The most certain item in citizen science fungal data is the fruit body occurrence in space and time (after cleaning). Thus, we decided to use the fruiting record as species identification is often incorrect in citizen science data (Andrew et al., 2017; Callaghan et al., 2021). For the lifestyle assignment, we used the genus level. The probability that a genus is identified incorrectly is far less likely than a species (currently ca. 1,147 genera and 21,000 species (Hibbett et al., 2014)). A random draw of 100 images revealed one misidentified genus. Please note that we focused our main interpretations on the full dataset. Results are consistent with findings based on species numbers for the northern biome, that is with both spring and fall fruiting peaks (Boddy et al., 2014). (4) The pattern may be affected by climate warming. We used two data subsets 1977–2000 and 2000–2021, where the effect of climate warming was less strong than in the full analysis and found consistent cyclic cubic fruiting splines (Tables S1–S3). Note that the temporal resolution of data in the tropical biomes was insufficient for time-series analyses.

Conclusion

Our results suggest a climate-driven fungal fruiting behaviour. With global warming leading to large-scale reorganization of climate zones (Cui et al., 2021) and increasing temperature variability (Tamarin-Brodsky

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et al., 2020), we expect changes in the spatiotemporal performance of fruit body-forming fungi, which may affect terrestrial carbon cycling (Luo, 2007) and organisms dependent on fungi-mediated food webs. Our data also highlights that long-term, well-replicated fungal phenology projects are important to cover entire biomes.

AUTHOR CONTRIBUTIONS

FSK and CB had the original idea. FSK conducted analyses and wrote the first draft of the manuscript. CB and UB helped interpret the results and contributed to writing the manuscript.

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CONFLICT OF INTEREST STATEMENT

No competing interests.

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DATA AVAILABILITY STATEMENT

The raw data for this study are available via GBIF (doi: 10.15468/dl.wwr3yt). The generated dataset that supports the findings of this study are openly available in DRYAD at https://doi.org/10.5061/dryad.1vhhmgqz2.

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