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Trait-dependent distributional shifts in fruiting of common British fungi

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AUTHORSHIP

EH, HK, and CA designed the study, CA and PMK collated the database and resolved taxonomy, EH and JD conducted statistical analyses. ACG and EH wrote the manuscript, with substantial contributions from all authors.

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Abstract

Despite the dramatic phenological responses of fungal fruiting to recent climate warming, it is unknown whether spatial distributions of fungi have changed and to what extent such changes are influenced by fungal traits, such as ectomycorrhizal (ECM) or saprotrophic lifestyles, spore characteristics, or fruit body size.

Our overall aim was to understand how climate and fungal traits determine whether and how species-specific fungal fruit body abundances have shifted across latitudes over time, using the UK national database of fruiting records. The data employed were recorded over 45 years (1970 – 2014), and include 853,278 records of Agaricales, Boletales and Russulales, though we focus only on the most common species (with more than 3,000 records each). The georeferenced observations were analysed by a Bayesian inference as a Gaussian Additive Model with a specification following a joint species distribution model. We used an offset, random contributions and fixed effects to isolate different potential biases from the trait-specific interactions with latitude/climate and time. Our main aim was assessed by examination of the three-way-interaction of trait, predictor (latitude or climate) and time.

The results show a strong trait-specific shift in latitudinal abundance through time, as ECM species have become more abundant relative to saprotrophic species in the north. Along precipitation gradients, phenology was important, in that species with shorter fruiting seasons have declined markedly in abundance in oceanic regions, whereas species with longer seasons have become relatively more common overall. These changes in fruit body distributions are correlated with temperature and rainfall, which act directly on both saprotrophic and ECM fungi, and also indirectly on ECM fungi, through altered photosynthate allocation from their hosts. If these distributional changes reflect fungal activity, there will be important consequences for the responses of forest ecosystems to changing climate, through effects on primary production and nutrient cycling.

Mounting evidence shows that changes in global climate have large effects on the phenology, abundance and distribution of plant and animal species (Feehan et al. 2009). With plants, earlier leafing in spring and/or later leaf senescence in autumn prolongs the growing season (Menzel and Fabian 1999, Fitter and Fitter 2002), with subsequent effects on the productivity and functioning of ecosystems, such as forests (Richardson et al. 2010).

Recent studies have shown that fungi too are highly responsive to changing climates, measured by fruit body appearance (Kauserud et al. 2012, Boddy et al. 2014, Büntgen et al. 2015). Shifts in the first and last dates of mushroom appearance have resulted in an extension of the autumnal fruiting season in the UK, and increased spring fruiting (Gange et al. 2007). These phenological changes reflect altered fungal activity, with consequences for forest ecosystem functioning, as fungi provide essential services such as decomposition, nutrient cycling and the formation of ectomycorrhizal (ECM) fungal mutualisms (Primicia et al. 2016).

Another consequence of a warming climate is a change in the spatial distribution of organisms, along altitudinal (Wilson et al. 2005) or latitudinal gradients (Hickling et al. 2006, Chen et al. 2011). However, fungi are conspicuously absent from such analyses, with just two notable exceptions. Yan et al. (2017), using species distribution modelling, predict that the distribution range in Tibet of the economically valuable Chinese caterpillar fungus (*Ophiocordyceps sinensis*) will decrease with climate warming. Meanwhile, using a global dataset of crop pest and pathogen records, Bebber et al. (2013) documented significant poleward shifts for many disease-causing fungi since 1960. Intriguingly, the northward shift by pathogens began in the late 1970s, mirroring increasing temperatures and the expansion of the overall UK fungal fruiting season (Gange et al. 2007). Given that we now know how fungal phenology responds to climate warming (Boddy et al. 2014), it is timely to assess if changes in the distribution of saprotrophic and ectomycorrhizal fungi have also occurred. To predict community responses to climate change, we need a better understanding of how species' abundances change (Johnson et al. 2013), and studying fungal distributions is critical for understanding how these organisms influence ecosystem responses to climate change (Mohan et al. 2014).

Ectomycorrhizal and saprotrophic fungi co-occur in woodlands, but differ in their nutritional mode and other life history traits (Bässler et al. 2015). Changes in spatial distributions of ECM fungi could be constrained, if there is a level of specificity between fungus and host and/or if the distribution of the host is limiting (Vellinga et al. 2009). Saprotrophs may also be constrained by host distributions (Heilmann-Clausen et al. 2016). Meanwhile, there is evidence that some ECM species can associate with novel hosts, facilitating range expansion and invasion into new habitats (Wolfe and Pringle 2012). Range expansions may lead on to fungal species becoming invasive (Kauserud et al. 2007, Gladieux et al. 2015). Furthermore, interactions between saprotrophic and ECM fungi can contribute to the structuring of fungal communities (Leake et al. 2002), with important ecosystem-level consequences (Fernandez and Kennedy 2016). Thus, understanding if changes in fungal phenology lead to changes in abundance at range edges, and ultimately shifts in distributions, is an essential, but unresolved, part of determining the fungal role in climate effects at the ecosystem level.

A fundamental goal of community ecology is to understand the distribution and abundance of organisms in time and space. Against a backdrop of climate change, the amount of information required for such analyses at the community level can be colossal, given that species show individualistic responses to climate in ecological and evolutionary time (Stewart 2009, Buckley and Kingsolver 2012). There is evidence that a trait-based approach can be of use in understanding both distribution and range shifts (Angert et al. 2011), though this has yet to be applied to fungi. Such an approach is timely, given recent syntheses of trait-based approaches in mycology (Crowther et al. 2014, Aguilar-Trigueros et al. 2015) and evidence of climate-driven reproductive trait selection in fungal communities (Andrew et al. 2016). Ultimately, a trait-based approach should enable a better understanding of processes in fungal biogeography (Martiny et al. 2006, Crowther et al. 2014). Thus, a trait-based approach provides a realistic way of testing if and how climate affects fungal abundance at the edges of ranges. Several reproductive traits related to fruit body and spore characteristics are thought to be influenced by climate variability, and may ultimately affect distributions (Kauserud et al. 2010, Andrew et al. 2016). More water is required to produce larger fruit bodies and spores, but larger spores could also be required in drier environments for germination. Dark melanised spores have better protection against UV and may, together with thick-walled spores, survive and spread further than light spores. Several other traits affect dispersal, which again can be relevant for how quickly fungi respond to climate with shifts in distributions. Larger fruit bodies produce more spores and fruit bodies with longer stipes could spread spores more distantly. In theory, smaller spores spread farther than larger ones (Norros et al. 2014) and the exterior ornamentation may also influence the aerodynamics of spores and their dispersal ability (Halbwachs and Bässler 2015).

The scarcity of studies in fungal biogeography is due in part to the fungi being invisible within substrata for long periods of time and the difficulty in characterising the huge diversity of fungi within ecosystems. While such problems become tractable using molecular methods (Tedersoo et al. 2014), these techniques cannot readily document any historical changes in fungal distributions. However, as with plant pathogens, databases of fungal occurrence can provide excellent records of presence and can be used to document changes in time and space (Bebber et al. 2013, Schenk-Jäger et al. 2016). In this study, we used a unique database of fruit body records from the UK, termed the Fungal Records Database of the British Isles (FRDBI) (http://www.fieldmycology.net/FRDBI/FRDBI.asp). The snapshot of the database was taken on 16 December 2015 and it then included 2,083,352 records of the fruiting of 14,146 species from 1669 to the present day, collected by amateur naturalists (citizen scientists), professional mycologists and scientific organisations.

Here, we use this database to examine whether changes in the latitudinal abundance of fruit bodies of ECM and saprotrophic fungi have occurred over the last 45 years in the UK. We address two specific questions: (1) has the UK latitudinal gradient in fungal abundance changed over time in a trait-specific way? and (2) are temporal shifts in fungal abundance associated with climate change? Our overall hypothesis was that changes depend on fungal traits and differ between ECM and saprotrophic species (Halbwachs et al. 2015), given that characteristics such as nutritional mode and spore size are important in determining fungal responses to climate (Damialis et al. 2015, Andrew et al. 2016). Furthermore, we hypothesized that ECM species would show fewer changes in fruiting distributions compared to saprotrophic species, because any changes in ECM fruiting will be largely dependent on changes in their host trees (Primicia et al. 2016).

Methods

Data characteristics

The data set comprised a compilation of fungal fruit body occurrence recorded throughout mainland Britain. Most records provide a collecting date and location (latitude and longitude). Many records before 1970 are deficient in some aspect (missing date or location) and we therefore used data from 1970 to 2014, which make up 84% of the full data set. From this reduced set, we extracted fruiting records of the agaricoid and boletoid members of the Agaricales, Boletales and Russulales, comprising in total 853,278 records of 2,844 species. Using this information, we obtained species’ prevalence and recording intensities within each of the 112 Watsonian vice-counties (VC) that map the UK, for every year (Fig. S1). We chose to use VC instead of gridded representation as much of the older data are at this level and this enabled us to obtain estimates of recording intensities over time. This also guided our choice of using a first order conditional autoregressive procedure rather than trying a point pattern approach with spatial Gaussian fields defined (Blangiardo & Cameletti 2015). For analytical purposes and to reduce recording bias to a minimum, we selected common (with more than 3,000 records each) and widely distributed ECM and saprotrophic species that are easy to distinguish in the field (avoiding potential misidentification), with an ephemeral fleshy fruit body. Further, we eliminated species with long-lived fruit bodies or which are parasitic. The resulting data comprised 304,121 records of 61 (21 ECM, 40 saprotrophic) species.

Fungal traits

Information on seven traits was taken from Knudsen and Vesterholt (2012): functional group (ECM versus saprotrophic), cap size, stipe height, spore volume, spore colour, spore wall thickness, and spore wall ornamentation. In addition, average fruiting day and standard deviation of fruiting day (a measure of season length) of each species were calculated from the data. The traits and correlations between them are explained and listed by species in Table S1 and Figures S1.1-S1.5.

Latitude and climate

The individual statistical unit in our analyses is the abundance of a species in a VC each year. For each VC and year, we calculated each species' average geographical position, measured by latitude and longitude. Annual mean temperature and annual total precipitation data for each record were obtained from the UK Meteorological Office, (http://www.metoffice.gov.uk/climate). These data were taken from the nine climate regions of the UK, as defined by the Meteorological Office. While we appreciate that higher resolution data may have provided more accurate representations of climate, such data were not available for the time period covered by this study. Combining the annual temperature and precipitation with the temperature difference between coldest and warmest month, we calculated a hygrothermic index (HT) reflecting the transition from continental (low values) to oceanic climate conditions (Lisewski and Ellis 2010):

$$HT = \frac{P * T}{10 * (T_H - T_C)}$$

where P is annual precipitation (mm), T is annual mean temperature, and T_H and T_C are monthly mean temperature in the hottest and coldest months, respectively.

Statistical analyses

The overall goal of the statistical modelling was to quantify how species-specific abundances have changed over time across the latitudinal gradient, and to evaluate how species' traits and climate have influenced these changes. Our approach is an extension of the Community Assembly via Trait Selection (CATS) (Warton et al. 2015) following a multivariate regression specification (Jamil et al. 2013, ter Braak et al. 2017) and a joint species distribution model specification (Pollock et al. 2014, Ovaskainen et al. 2016). The key objectives were to obtain parametric estimates of how traits affected the latitudinal and climatic gradient in abundances over time, while also accounting for potential biases associated with multivariate presence-only data and uneven spatial and temporal sampling intensity.

To assess how abundance changes with time and latitude or climate, and whether changes are associated with specific traits, we compiled the number of fruit body records (y_{ijk}) for each species i, in VC *j* (112 VCs), and year *k* (1970 to 2014). Because of the complex structure of the data, we used hierarchical Bayesian models (Gelman et al. 2004), fitted using the Integrated Nested Laplace Approximation, INLA (Table S3) (Rue et al. 2009). Because the response data (y_{ijk}) are discrete counts and over-dispersed relative to a Poisson distribution, we assumed a negative binomial likelihood with a logarithmic link to a linear predictor:

$$y_{ijk}|\theta_{ijk},\varphi_{ijk} \sim NB(\mu_{ijk},n)$$

$$log(\mu_{ijk}) = \eta_{ijk}$$

Here θ denotes all parameters describing the mean, μ, and φ denotes the hyper-parameters associated with parameter distributions. The parameter n denotes the negative binomial size, which quantifies the degree of overdispersion.

Within the linear predictor (η_{ijk}), we specify parametric relationships with predictors (time, latitude, climate and traits) and several potential sources of bias common to datasets such as this, including: (i) different likelihoods of species being collected because of recorder bias; (ii) yearly differences in sampling intensities; (iii) spatial biases due to where observers tend to search and (iv) the different sizes of VCs. These potential biases were incorporated using an offset and by a number of random effects (described in detail below) as follows, where *i* = species, *j* = VC, and *k* = year:

$$\eta_{ijk} = log(q_i E_{jk}) + t_k + v_j + u_j +$$

$$\beta_0 + b_{0i} + (\beta_1 + b_{1i}) \cdot x_j + (\beta_2 + b_{2i}) \cdot time_k + (\beta_3 + b_{3i}) \cdot x_j \cdot time_k +$$

$$\beta_4 trait_i + \beta_5 x_j \cdot trait_i + \beta_6 time_k \cdot trait_i + \beta_7 x_j \cdot time_k \cdot trait_i$$

We defined species' prevalence (q_i) as the probability that a record selected at random from the full species pool belongs to species *i*. To account for variable sampling intensities both among years and between VCs, we included the sampling volume, defined as the number of records of all species for every year in each VC, E_{jk}, which is referred to as recording intensity per VC per year. This was combined with the species-specific prevalence in calculating the expected number of records per species per VC per year (q_iE_{jk}). Using $\log(q_iE_{jk})$ as an offset brings the analysis into the realm of density, i.e., abundance relative to the expected number of records per species per VC per year. The logarithm was applied due to the log-link function between the linear predictor and the mean (μ_{ijk}).

Subsequently, because the records were structured by year, and needed to be grouped across a VC, we included an exchangeable random contribution for the year (t_k). Note that year as a linear term was used as part of the fixed effect in this study. Furthermore, the VCs are spatially positioned discrete units, so we included an exchangeable random contribution of the VCs (v_j) and neighbouring VCs (u_j). This neighbourhood structure was modelled as a Conditional Autoregressive Process (CAR) using a first-order neighbouring graph (Besag 1974), following the Besag-York-Mollie (BYM) model of spatial contribution (Blangiardo and Cameletti 2015).

To accommodate species-specific responses to the predictor variables (x_j), we included species-specific random effects of intercept (b_{0i}), the predictor variable (b_{1i}), the time variable (b_{2i}) and the interaction between the predictor variable and the time (b_{3i}).

Finally, the β's were the fixed effects answering the main aims of the study, including how abundances are related to the effects (β_1 to β_3) of time and predictors (x_j = latitude or climate) as well as their interactions, while β_4 to β_7 represent effects associated specifically with the investigated traits. Herein, β_7 is the trait-specific effect on how the gradient along the predictor changes with time, i.e., our main focus. In the study, each trait was analysed separately, and each of the predictor variables, i.e. latitude, temperature, precipitation and HT, was included separately, whereas time was always included. This produced 36 separate models, exploring all combinations of the four predictor variables with each of the nine trait variables.

In summary, the structure of the data necessitated a complex model specification with terms associated with biases and nuisance information (log(qE), β_0, β_1, β_2 and β_3), with dependencies of the observations (t_k, v_j and u_j), with species-specific random contribution of terms (b_{0i}, b_{1i}, b_{2i} and b_{3i}), and finally the fixed effects of traits (β_4, β_5, β_6 and β_7).

We used Gaussian weak priors for all fixed effects (β's), and log-gamma priors for the hyper-parameters of negative binomial size (n), the exchangeable VC contribution (v_j), the spatial VC contribution (u_j) and the temporal exchangeable contribution (t_k). For the species-specific random contribution we were able to reduce a multivariate Wishart distribution prior to a set of univariate random contributions with individual priors of a log-gamma distribution. This reduction was possible when we used one predictor at a time and rescaled the predictor variables and the time vector to zero mean and unit variance prior to analysis. Factorial traits were analysed as a treatment contrast. All analyses were performed with the INLA package (Rue et al. 2009) in R v. 3.3.1 (R Core Team 2016).

Results

Distribution of records within the dataset

The number of records per VC of the 61 focal species showed a spatial differentiation but lacked an obvious latitudinal pattern (Fig. S1a). There was also a relatively even coverage in species richness per VC for these 61 species (Fig. S1b) and almost all species were present in every VC. Meanwhile, the average abundance per species per VC over time did not show an even pattern (Fig. S1c), with ‘hotspots’ of collection in some areas.

Latitudinal changes in abundance

To set the scene for assessing the trait-specific effects we illustrate the relative trend of the focal species as a group relative to the less frequent species, i.e. those included in the full species pool. This information may be interpreted as bias and therefore we needed to isolate it from the information carried by the interactions involving the traits. In this we found a clear negative main effect of time ($p < 0.001$), showing that recordings of the most common species have declined in average abundance over time (Fig. 1, Table S2), and this decline was consistent across all trait groups (Table S2). However, there was also a significant positive latitude:time interaction term (probability of being positive = 0.953), indicating that the decline in abundance of common species was less at higher latitudes (Fig. 1, Table S2).

The three-way interaction term between latitude, time, and nutritional mode was highly significant (probability of coefficient being positive < 0.001, Fig. 1, Table S2, S3), indicating that changes in abundance over time differ between ECM and saprotrophic species. As a result of this significant interaction, the modelled abundances over time and across latitudes were remarkably different for ECM (Fig. 2a) and saprotrophic species (Fig. 2b). Abundance of ECM species was relatively low in the north, but the trend has been toward increasing abundances in this area. However, in the southern region there was a marked decline in average abundance relative to the saprotrophic species over time (Fig. 2a). Meanwhile, the saprotrophic species had a more even latitudinal abundance in the early period of records than

ECM species, but have declined in abundance in both the north and south, with the decline in the north more pronounced (Fig. 2b). This pattern indicates that today it is more common to record ECM species in northern parts of the UK, whereas in the south the higher average abundance of ECM records seen in the past has declined to a level similar to or lower than that of the saprotrophic species.

The probabilities associated with coefficients being positive are depicted in Fig. 3 and 95% credibility intervals are presented in Table S2. Three of the three-way interaction terms (Latitude:Time:Trait) are noteworthy here. Firstly, cap area showed a significant positive coefficient (Fig. 4a). The abundance of species with small caps was relatively evenly distributed from south to north at the start of the study period. The lack of a latitudinal trend persisted through time, but the abundance of small-capped fungi decreased over time. Species with larger caps, on the other hand, were previously more common in the south of the country than in the north. During the study period, this latitudinal abundance gradient shifted direction due to a strong decline in the south and a weak increase in the north (Fig. 4b).

Both spore-wall smoothness and length of the fruiting season (the standard deviation of fruiting day) have shown significant and similar latitudinal trends over time to that of functional group (Fig. 3). Fungal species with smooth spores are on average more frequently recorded today than previously, relative to species with ornamented spores (Table S2, Fig. 4c,d). There has been a strong change among the species with ornamented spores in the south, where they have shown a considerable drop in average abundance (Fig. 4c), compared with a weak increase in the north. Species with smooth spores have declined in relative abundance in both south and north, but the decline was more pronounced in the north (Fig 4d). Fruiting season width is another important parameter, and species with short seasons, (standard deviation of fruiting about 1 month), have become less abundant in the south, while maintaining their abundance in the north (Fig. 4e). However, species with long fruiting seasons, (standard deviation of about 2 months), have tended to become less abundant regardless of latitude, but with stronger declines in the north than in the south (Fig. 4f).

Finally, there was a weak tendency for species with thick-walled spores to be more abundant in the northern regions (‘Env:trait’ for ‘spore wall’ in Fig 3). However, this pattern did not change with time, as the three-way interaction (Latitude:Time:Trait) was not significant (Fig 3, Table S2).

Climatic gradients

Across the UK, temperatures decrease towards the north (Fig. S2a), and precipitation increases toward the west (Fig. S2b), while the hygrothermic index shows a southeast – northwest gradient (Fig. S2c). These three climate variables each showed different, complex relationships with fungal fruiting via both direct effects and through interactions with traits and time (Fig. 3).

We found a high probability ($p = 0.982$) that the three-way interaction of temperature:time:nutritional mode was positive, indicating that the influence of temperature over time differs between ECM and saprotrophs (Fig.3,Table S2). However, neither rainfall nor the hygrothermic index showed a change across latitudes over time. None of the three-way interactions involving rainfall were significant, suggesting that changes in abundance across latitude over time are not related to average annual precipitation alone.

Cap area, fruiting time and length of fruiting season all showed significant three-way interactions with the hygrothermic index (Fig 3, Table S2), with negative coefficients for cap area and average fruiting time and a positive coefficient for fruiting season. Overall, we found a high probability that later fruiting species occurred more frequently in more oceanic areas (probability of coefficient being positive = 0.989, Table S2). The trend for species with larger caps was similar, but weaker (probability of being positive = 0.786). However, over time, there has been a relative increase in abundance of later fruiters in more continental areas, relative to oceanic areas. This trend was less pronounced in the earlier fruiting species. Thus, over time, the relative difference between early and late fruiting species has reduced, leading to a high probability ($p = 0.998$) that the coefficient of the three way interaction was negative (Fig. 3, Table S2). For fruiting season length, we found a high certainty ($p = 1.000$) that the coefficient for the time:fruiting width was positive, i.e. that the temporal change in relative abundance depends on fruiting-season length. The species with broader fruiting seasons have become relatively more common compared with those of shorter fruiting-season length. The significant three-way interaction ($p = 0.996$, Table S2) suggests that this favouring of species with broader seasons has been particularly strong in regions with a high hygrothermic index (oceanic areas). However, there has been a dramatic decline in the relative abundance of the short seasoned species in the oceanic parts of UK.

Discussion

Over the last 45 y, there has been a significant change in the distribution of fungal fruiting in the UK and this change is clearly trait-specific, upholding our original hypothesis. Among the most frequently recorded fungal species, ECM fungi now fruit more prolifically in the north of the country than in the past, but less so in the south, while saprotrophic fungi fruit less commonly now in both areas. Changes in fungal fruiting over time are strongly related to climate (seen in the hygrothermic index), suggesting that both temperature and rainfall are responsible for these distributional changes in fungal fruiting, but in association with different sets of traits.

Our most important finding is that the abundance of ECM fungal fruiting has increased in more northerly latitudes and declined markedly in the south. This finding contradicts our hypothesis that ECM fungi might show few changes over time. Autumnal mean daily temperature and rainfall in the UK have increased over our study period, but more so in the north (Anonymous 2009). Such climatic changes may result in direct effects on the ECM fungi and also in indirect effects through enhanced growth and later leaf fall of their tree hosts (Gill et al. 2015). Delayed leaf senescence in autumn has been reported across Europe (Kolarova et al. 2014), and it is perhaps no coincidence that the most prevalent host for ECM fungi in the UK, *Quercus robur*, has shown the greatest growing-season elongation (of 18 common tree species) of 31 days, between 1976-2010 (Kolarova et al. 2014). As the carbon supply from the host may have a strong influence on ECM fungal fruiting (Egli et al. 2010, Büntgen et al. 2012b), we conclude that temperature-driven increases in resource allocation from host trees to ECM associates, coupled with enhanced autumnal soil moisture availability, are the most likely causes of increased fruiting of ECM fungi towards the north, corroborating results from Primicia et al (2016). The decline in ECM fungal fruiting in the south may be due more to rainfall than temperature. In the UK, over the time period covered by our study, rainfall in southern England in summer has decreased by 13%, while in the north of the UK, the decrease is only 2% (Anon. 2009). It is known that both ECM and saprotrophic fungal fruiting are related to prevailing weather conditions between April and August (Büntgen et al. 2013). Thus, ECM fungal fruiting may have decreased in the south because of insufficient rainfall prior to fruiting. This ecological response may be comparable to the drought-induced declines of edible mycorrhizal fungal harvests in the Mediterranean area (Büntgen et al. 2012a, 2015).

Meanwhile, saprotrophic species have shown a decline in fruiting in both the north and south, with the trend being strongest in the north. Like ECM, saprotrophic fungal fruiting is also thought to be influenced by temperature and moisture effects on the process of decomposition (Rousk and Bååth 2011, Büntgen et al. 2013). Moore et al. (2008) suggest that appearance of saprotrophic fruit bodies in autumn is related to rainfall in summer. Over the study period, there has been a weak trend for fewer days of rain during the summer, a trend which is stronger in the north of the country. However, in our study the precipitation is not strongly associated with nutritional mode, i.e. the response seen among saprotrophic species is mirrored by ECM species. Thus, the latitudinal trends in changes of abundance are likely to be more driven by temperature.

Resource availability, temperature and rainfall are just three of the factors that influence the start and end of a fungal fruiting season and it is certain that these factors are inter-dependent. The Hygrothermic Index (combining temperature and rainfall) was a major factor related to the fruiting time and width of the fruiting season. We found that species with broader seasons have become more frequently recorded, and that this effect was stronger in more oceanic parts of the country. Meanwhile a strong decline in short-season species has occurred in the more oceanic areas. Although the fruiting season of saprotrophs in the UK is generally longer than that of ECM fungi (Kauserud et al. 2012), the patterns seen with fruiting season length did not correspond with those seen in the nutritional modes. This suggests that there is an additional climatic force acting on the fruiting season length, in saprotrophic and ECM species alike. It is likely that resource availability and a sudden drop in temperature (e.g. frost) are likely to play significant roles in determining the end of a fruiting season (Gange et al. 2013). Autumnal frost frequency has declined over the study period, but whether the timing of frosts in different parts of the country has changed is less clear (Anonymous 2009). Whether short- and broad-season species are differentially susceptible to frost is also unknown, but possible (Ohenoja 1989).

In addition to nutritional mode, other traits were important for predicting changes in latitudinal abundance. Cap area was a particularly important trait, as species with larger caps have become more common in the north, while those with smaller caps have declined in abundance generally. ECM fungi produce larger caps than saprotrophic fungi (Bässler et al. 2015), a phenomenon thought to be driven by the receipt of carbon from the host. The change in ECM fungal fruiting in northern areas mirrors the changes in cap area and is further evidence for enhanced resource allocation from hosts leading to increased fruit body production. However, there is also an oceanic element, not correlated with nutritional mode, as smaller cap sizes seem to be positively influenced by oceanic climate relative to species with larger cap sizes. Although, large fruit bodies need large amounts of water to expand, so also do many small fruit bodies, and the greater reduction in rainfall seen in the south may be part of the explanation of why we observed a combination of a clear nutritional mode/cap-size differentiation northwards, but also a simultaneous association with a continental gradient and cap-sizes.

A similar trend was seen with spore surface traits. Species with ornamented spores have become more abundant in the north, while smooth-walled species have become less abundant overall. ECM species often have more ornamented spore walls than saprotrophic species (Halbwachs et al. 2015) and so these changes correlate with those for nutritional mode. However, spore colour and wall thickness traits showed little change over time.

It is not just temperature and rainfall that have changed over our study period. Important changes in atmospheric CO_2 levels and nitrogen deposition have occurred simultaneously and may all affect fruit body production of forest fungal species. Elevated CO_2 can lead to increased fruit body production of ECM species, through enhanced carbon supply via their hosts (Andrew and Lilleskov 2009, Godbold et al. 2015). Elevated CO_2 also results in altered leaf litter quality that slows decomposition (Cotrufo et al. 1994), though whether this results in reduced fruit body production of saprotrophic species is far less clear (Büntgen et al. 2013). High rates of N deposition reduce ECM fruit body production (Peter et al. 2001), and deposition rates have been higher in the south of the country over the study period (Fowler et al. 2004). Neither CO_2 nor N can fully explain the increase in ECM fruiting, but both may play a role in a complex array of atmospheric factors, all of which interact (Büntgen et al. 2013).

In any analysis of this type, the biases within such datasets must be considered. Large datasets assembled by a mixture of citizen scientists and professionals can be influenced heavily by the distribution and knowledge of recorders, the geographical structure of the landscape and spatial patterns of land use (Ward 2014, Mair and Ruete 2016). However, appropriate data management and statistical methods can still yield robust analyses of changes in fungal phenology and distributions (Boddy et al. 2014, Davis et al. 2015, Taheri et al. 2016). There are several arguments for our claim that the trends found here are not caused by inherent biases in the data. Firstly, we restricted our analysis to the last 45 years, when recording has been much more organised and coordinated, resulting in a relatively even distribution of records (see Supporting Information). Secondly, because rare species can be over-represented due to collector bias (Halme et al. 2012), we analysed only a subset of common species, each with a large number of records evenly distributed across the country. Thirdly, our models explicitly account for and identify the influences of species' prevalence, sampling effort, data structure and temporal changes in recording. The latter includes changes in human population sizes, number of recorders and differences in recording intensity and recorder specialisation. Moreover, if there was recorder bias, then ECM and saprotrophic species would show similar trends, as they fruit in the same locations, but they do not. Furthermore, we identified two broad-scale distinct biological phenomena: temperature-related changes in distributions of nutritional modes and precipitation-related changes in fruiting period, which in combination make changes in recorder specialisation unlikely. As these are trait-related, it also makes bias from climatic structure unlikely (Chapman 2010). Finally, changes in forestry practices over the last 45 years could introduce further biases. However, in this study very few fungal species are associated with actively managed coniferous plantations, with most records from less managed pine forests, and there has been relatively little change in the latitudinal distribution of broad-leaved woodlands across the UK over our study period (Quine et al. 2011).

In summary, it is clear that distributions of fungal fruiting have changed across the UK over the last 45 years, driven by two distinct trait specific processes acting on different climatic gradients. These changes may reflect altered resource acquisition patterns of both ECM and saprotrophic species (Bässler et al. 2016). Changes in fruiting presumably reflect changes in fungal activity, and such changes may affect ecosystem processes such as decomposition and nutrient cycling, which will have implications for the functioning and productivity of both broad-leaved forests and managed coniferous plantations (Fernandez and Kennedy 2016). Our study specifically focused on the most common species in the UK which show a decline in recording intensity relative to the less frequent species, but we do not believe that this will affect the generality of our results in the wider British mycobiota. This is because the species-specific traits show a stronger pattern than the identity of the species. For example, if a rare species has the same trait as one of the investigated common species, we can anticipate that its response will be similar to that common species, but different to an equally common one, with a different trait. Furthermore, we isolate/identify this type of bias by the main-effect of time in our models. Thus we suggest that the temperature and precipitation influences on fruiting processes are similar for the less frequent species, but this must be shown by future rigorous analyses. In addition, our results show that the exploration of historical databases to document changes in fungal fruiting abundance is a valuable approach for indicating how fungal communities may change in ecosystems such as forests, particularly in response to environmental change.

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Figure legends

Figure 1. The posterior distribution of the coefficients for the model including the functional groups, i.e. ECM vs saprotrophic. The darkness of the individual horizontal bars reflect the probabilities (dark = high). The centre point of the horizontal bars is the expected value, and the darkest bars are those with a significant effect, i.e. the 95% credibility interval excludes 0 (for no effect). The scale of the coefficients relates to a standard deviation change of the predictor variables. Each number in brackets corresponds to those in Table S2.

Figure 2**.** Diagrammatic representation of the modelled abundances over time and across latitude (northing) for hypothetical fungal species, each with a median prevalence of p=0.005, and for a mean of 1000 records per grid cell. (a) Expectation for the functional group ECM (b) Expectation for the functional group saprotroph. Degree of shading represents abundance, with dark colour indicating high abundance and vice versa.

Figure 3. A colour chart depicting interaction effects of the different traits with and climate and latitude. Each trait is listed in the left of the figure. 'Env' in each legend corresponds to the particular variable: Latitude, Temperature, Rainfall or Hygrothermic Index (HT). Red colours indicate a positive expected effect, whereas blue colours indicate negative effects. The intensity of the colours correspond to the probability of being either negative or positive. The stars relate to the credibility interval of the effects * p = 0.9, ** p = 0.95, and *** p = 0.99. See also Table S2 for the actual 95% credibility intervals associated with these effects; those depicted here are the coefficients labelled 3, 5, 6 and 7 of latitude, temperature, rainfall and Hygrothermic Index (HT) from Table S2. These are the coefficients that specifically address trait-dependent distributional shifts among fruiting records in UK.

Figure 4**.** Diagrammatic representation of the modelled abundances over time and across latitude (northing) for hypothetical fungal species, each with a median prevalence of p=0.005, and for a mean of 1000 records per grid cell. Expectation for species with: (a) small caps, (b) large caps, (c) ornamented spores, (d) smooth spores, (e) species with short and (f) species with long fruiting seasons. Darker shading indicates higher abundance.

Supplementary Information

Table S1. List of species used in the analysis, with data for their different traits and summary statistics for the relationship between the traits (Figures S1.1-1.5).

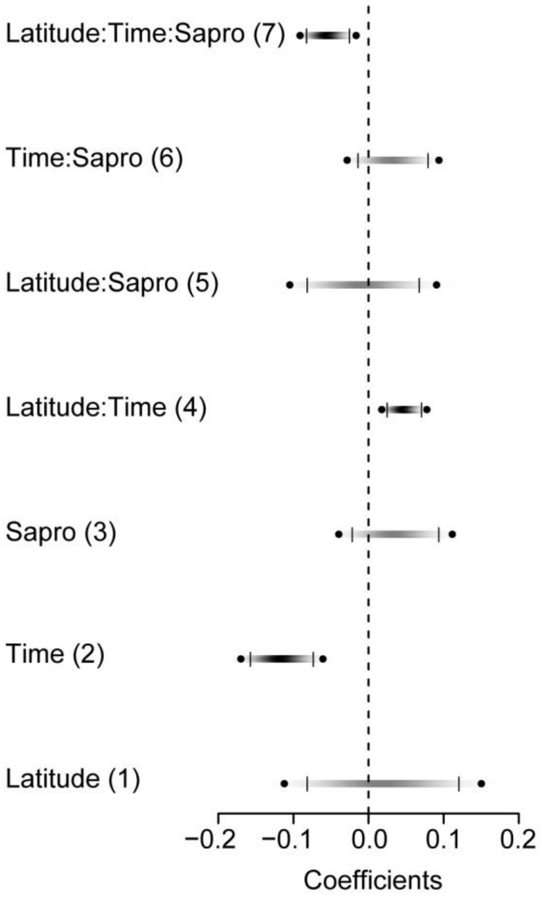
Table S2. Table of 95 % credibility intervals for different terms in the fitted models.

Table S3. A brief outline of the INLA analysis and output for the trait nutritional mode.

Figure S1. Distribution of records in the dataset across Vice Counties. a) Log number of records; b) Number of species; c) Average abundance per species per year. The left hand vertical axis on (a) and (c) depicts latitude.

Figure S2. Climatic data across Vice Counties. a) Mean annual temperature (°C), b) Mean annual precipitation (mm), c) Hygrothermic Index, higher values represent oceanic climate, lower value a more continental climate. The left hand vertical axis on (a) and (c) depicts latitude.

Figure 1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Time:Sapro (6)
Latitude:Sapro (5)
Latitude:Time (4)
Sapro (3)
Time (2)
Latitude (1)
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−0.1
0.0
0.1
0.2
Coefficients

Figure 2

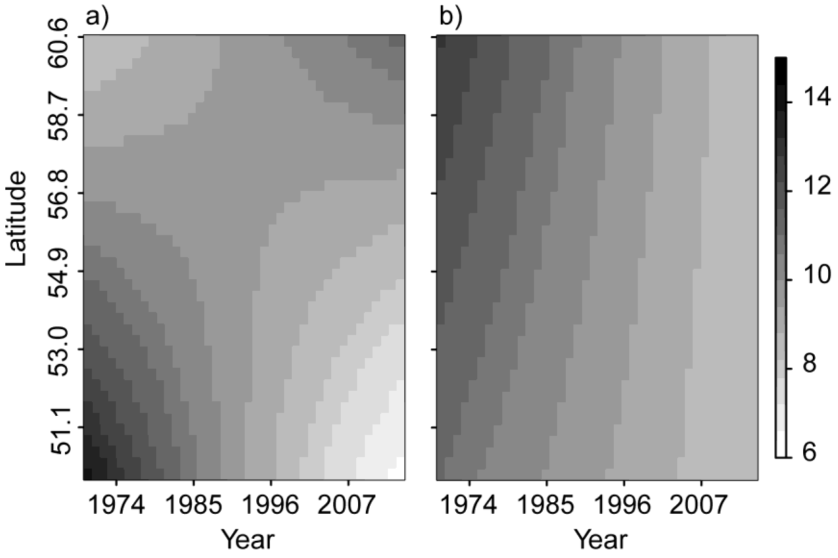


Figure 3

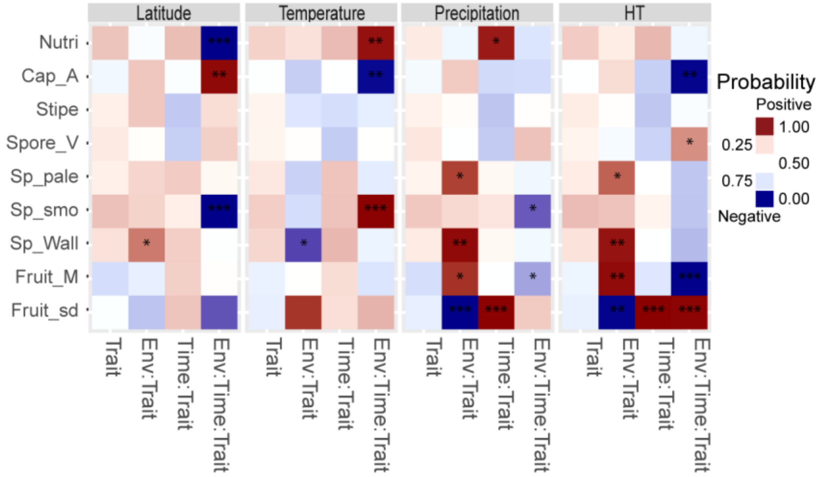
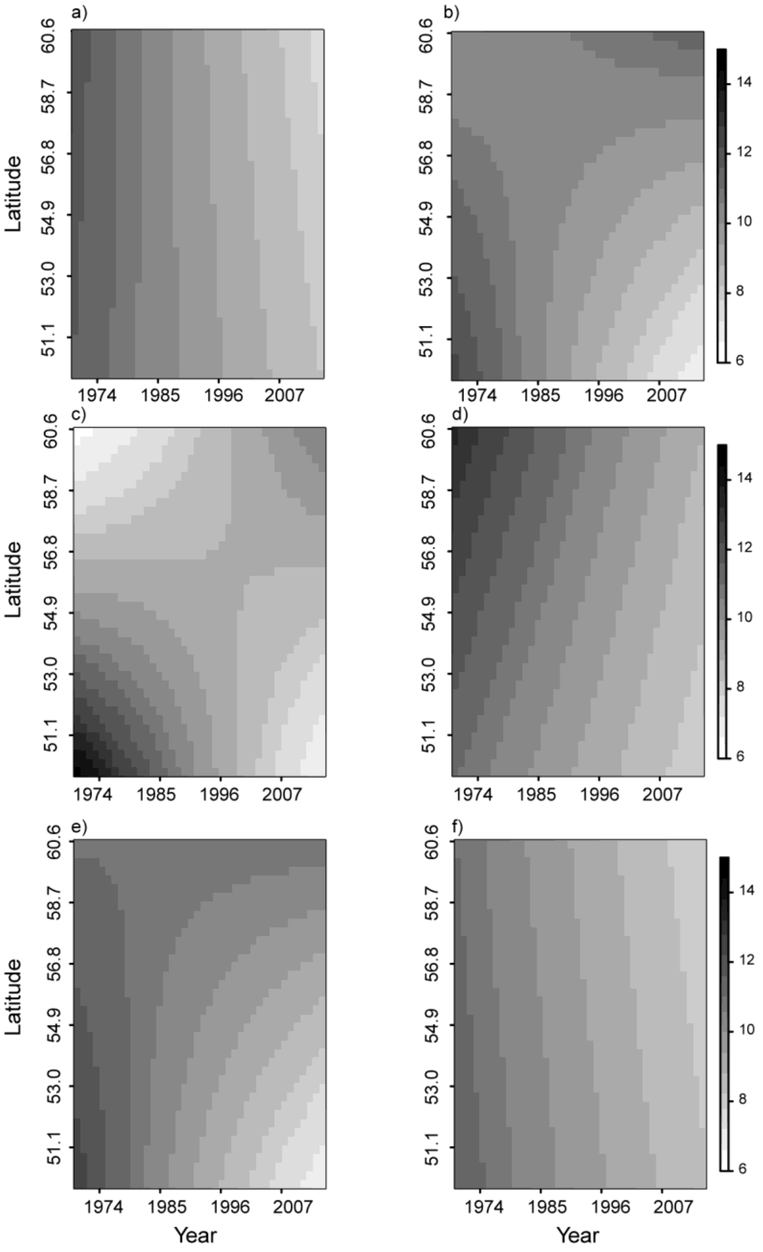


Figure 4


a)
b)
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Latitude
60.6
58.7
56.8
54.9
53.0
51.1
1974
1985
1996
2007
Year
14
12
10
8
6

ies	Nutri. Mode	Stipe mean	Stipe max	Cap area	Spore vol.	log(Vol)	Spore colour	Spore wall	Spore smooth	Fruiting mean	Fruiting SD
nita citrina	ECM	80	120	3318.31	37.70	3.63	pale	thin	TRUE	280.01	23.61
nita fulva	ECM	125	180	2375.83	63.36	4.15	pale	thin	TRUE	254.17	32.29
nita muscaria	ECM	165	250	13273.23	30.63	3.42	pale	thin	TRUE	281.68	25.28
nita rubescens	ECM	105	150	7853.98	28.93	3.36	pale	thin	TRUE	258.37	38.18
bitius titubans	Sap	62.5	100	706.86	46.50	3.84	dark	thick	TRUE	241.89	63.37
tus edulis	ECM	95	150	12271.85	42.61	3.75	dark	thick	TRUE	267.75	28.19
rophyllum rachodes	Sap	115	200	11309.73	37.99	3.64	pale	thick	TRUE	281.20	41.62
ocybe fragrans	Sap	42.5	60	433.74	17.25	2.85	pale	thin	TRUE	262.82	91.22
ocybe nebularis	Sap	75	90	7088.22	14.24	2.66	pale	thin	TRUE	299.12	33.50
rinellus micaceus	Sap	70	100	213.82	24.05	3.18	dark	thick	TRUE	245.39	79.81
rinopsis atramentaria	Sap	110	170	1963.50	27.36	3.31	dark	thick	TRUE	256.88	69.13
rinus comatus	Sap	175	300	1590.43	43.66	3.78	dark	thick	TRUE	276.59	39.25
nophyllus pratensis	Sap	90	150	4417.86	14.14	2.65	pale	thin	TRUE	289.90	33.50
nophyllus virgineus	Sap	40	60	1256.64	19.27	2.96	pale	thin	TRUE	297.02	28.38
mmulina velutipes	Sap	45	80	881.41	14.20	2.65	pale	thin	TRUE	183.90	138.30
phorus psittacinus	Sap	40	60	829.58	23.76	3.17	pale	thin	TRUE	287.13	37.77
nopilus penetrans	Sap	50	80	1963.50	19.90	2.99	dark	thick	FALSE	283.06	47.13
nopus confluens	Sap	85	120	593.96	13.29	2.59	pale	thin	TRUE	264.75	35.93
nopus dryophilus	Sap	75	120	962.11	9.36	2.24	pale	thin	TRUE	259.82	44.11
nopus peronatus	Sap	52.5	75	1418.63	16.49	2.80	pale	thin	TRUE	269.56	37.12
eloma crustuliniforme	ECM	47.5	70	2827.43	33.12	3.50	dark	thick	FALSE	283.32	26.41
rocybe chlorophana	Sap	50	80	1590.43	19.90	2.99	pale	thin	TRUE	285.74	34.23
rocybe conica	Sap	67.5	120	2164.75	27.85	3.33	pale	thin	TRUE	273.66	34.30
rophoropsis aurantiaca	Sap	25	40	2375.83	10.54	2.35	pale	thin	TRUE	278.79	35.41
henopellis radicata	Sap	150	250	3578.47	87.31	4.47	pale	thin	TRUE	267.58	36.90
holoma fasciculare	Sap	55	80	962.11	15.58	2.75	dark	thick	TRUE	257.53	66.89
ria badia	ECM	80	120	7853.98	31.81	3.46	dark	thick	FALSE	273.89	31.13
ybe geophylla	ECM	32.5	50	397.61	25.92	3.25	dark	thick	TRUE	277.11	31.24

caria amethystina	ECM	55	80	490.87	41.23	3.72	pale	thick	FALSE	280.74	28.00
caria laccata	ECM	45	70	490.87	41.04	3.71	pale	thick	FALSE	273.07	40.31
arius quietus	ECM	50	70	2164.75	25.36	3.23	pale	thin	FALSE	276.52	27.57
arius subdulcis	ECM	45	65	1104.47	28.08	3.33	pale	thin	FALSE	277.73	33.63
arius tabidus	ECM	50	80	490.87	22.78	3.13	pale	thin	FALSE	273.42	30.84
arius turpis	ECM	42.5	65	5674.50	23.33	3.15	pale	thin	FALSE	280.36	24.30
cinum scabrum	ECM	135	200	7853.98	48.96	3.89	pale	thick	TRUE	268.51	28.24
ota cristata	Sap	42.5	70	1590.43	11.00	2.40	pale	thick	TRUE	273.87	36.60
sta nuda	Sap	70	90	7853.98	17.08	2.84	pale	thin	FALSE	291.93	62.64
perdon perlatum	Sap	52.5	75	1772.05	8.25	2.11	dark	thick	TRUE	270.47	58.34
perdon pyriforme	Sap	32.5	45	706.86	7.07	1.96	dark	thick	TRUE	256.75	77.26
asmiellus ramealis	Sap	12.5	20	122.72	16.95	2.83	pale	thin	TRUE	271.63	46.16
asmius oreades	Sap	60	80	706.86	24.87	3.21	pale	thin	TRUE	243.50	55.87
ena galericulata	Sap	115	200	593.96	42.61	3.75	pale	thin	TRUE	278.50	56.65
ena galopus	Sap	65	80	176.71	34.56	3.54	pale	thin	TRUE	282.28	37.73
ena inclinata	Sap	70	110	397.61	30.63	3.42	pale	thin	TRUE	289.64	45.50
ena pura	Sap	65	100	706.86	11.91	2.48	pale	thin	TRUE	282.13	36.46
ena vitilis	Sap	70	90	122.72	31.91	3.46	pale	thin	TRUE	283.82	49.31
lepista flaccida	Sap	35	50	3318.31	8.84	2.18	pale	thin	FALSE	287.95	57.91
sola plicatilis	Sap	75	120	38.48	56.12	4.03	dark	thick	TRUE	250.22	58.65
llus involutus	ECM	70	100	7088.22	27.10	3.30	dark	thin	TRUE	272.77	31.21
eus cervinus	Sap	70	100	5674.50	20.88	3.04	pale	thick	TRUE	257.31	53.12
hyrella candolleana	Sap	70	100	2827.43	20.52	3.02	dark	thick	TRUE	233.06	56.93
hyrella piluliformis	Sap	65	90	1963.50	10.08	2.31	dark	thick	TRUE	275.71	55.65
docollybia butyracea	Sap	65	90	2375.83	13.74	2.62	pale	thin	TRUE	290.19	51.94
docollybia maculata	Sap	100	150	3848.45	15.71	2.75	pale	thin	TRUE	276.68	27.13
sula atropurpurea	ECM	45	60	3848.45	26.38	3.27	pale	thin	FALSE	272.06	30.67
sula cyanoxantha	ECM	75	100	7853.98	28.27	3.34	pale	thin	FALSE	259.20	36.03
sula nigricans	ECM	50	70	13273.23	24.67	3.21	pale	thin	FALSE	270.08	34.82
sula ochroleuca	ECM	50	70	5674.50	35.34	3.57	pale	thin	FALSE	276.64	30.49
holomopsis rutilans	Sap	80	120	5674.50	18.56	2.92	pale	thin	TRUE	274.84	30.80

aria furfuracea	Sap	27.5	40	363.05	22.68	3.12	dark	thick	TRUE	219.73	119.12
ocomellus chrysenteron	ECM	65	100	4417.86	36.00	3.58	dark	thick	FALSE	262.08	35.03

Table S1. The 61 species used in the analysis, with information on their Nutritional mode (Nutri mode) (Ectomycorrhizal (ECM) or saprotrophic (Sap), mean and maximum stipe height (in mm), cap area (in mm^2), spore volume (µ^3), spore colour, spore wall thickness, spore smoothness, mean fruiting day and standard deviation of fruiting day.

Relationships between traits

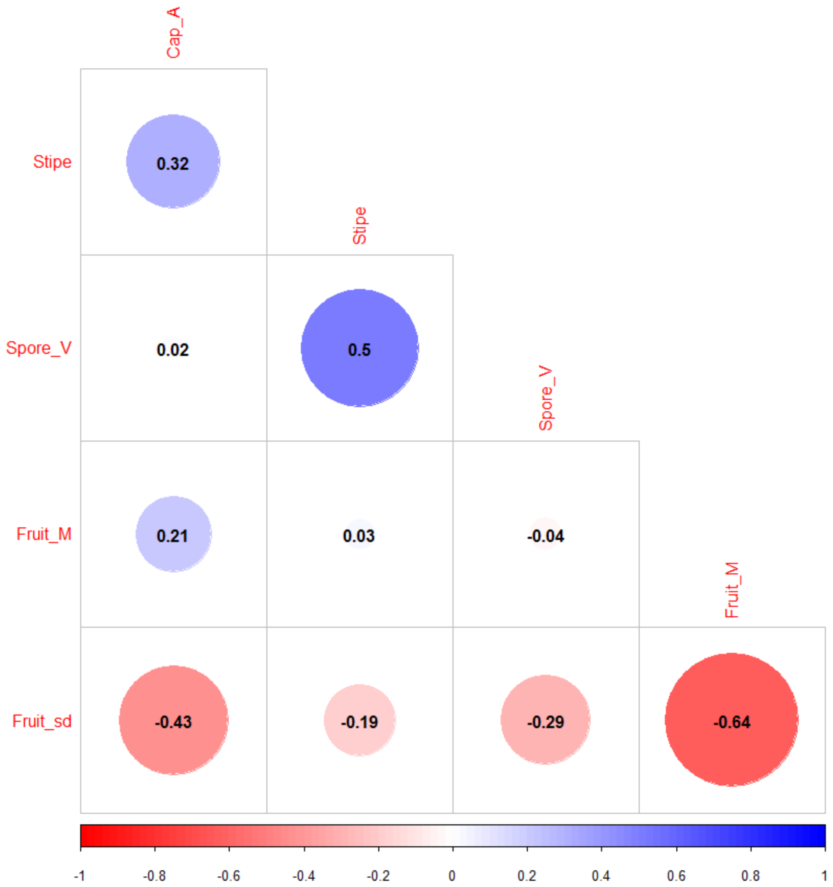

Figure S1.1 The correlation values between the continuous traits.

Chi-square tests of categorical traits, only significant listed:

```
Nutritional mode vs spore_smooth:

          Spore_smooth
Nutri_Mode FALSE TRUE
       ECM    13    8
       Sap     3   37


        Pearson's Chi-squared test with Yates' continuity correction

data:  table(Nutri_Mode, Spore_smooth)
X-squared = 18.347, df = 1, p-value = 1.841e-05
```

Spore wall vs spore colour

```
            Spore_wall
Spore_colour thick thin
        dark    17    1
        pale     6   37

        Pearson's Chi-squared test with Yates' continuity correction

data:  table(Spore_colour, Spore_wall)
X-squared = 31.656, df = 1, p-value = 1.841e-08
```

Boxplot of continuous traits against categorical traits:

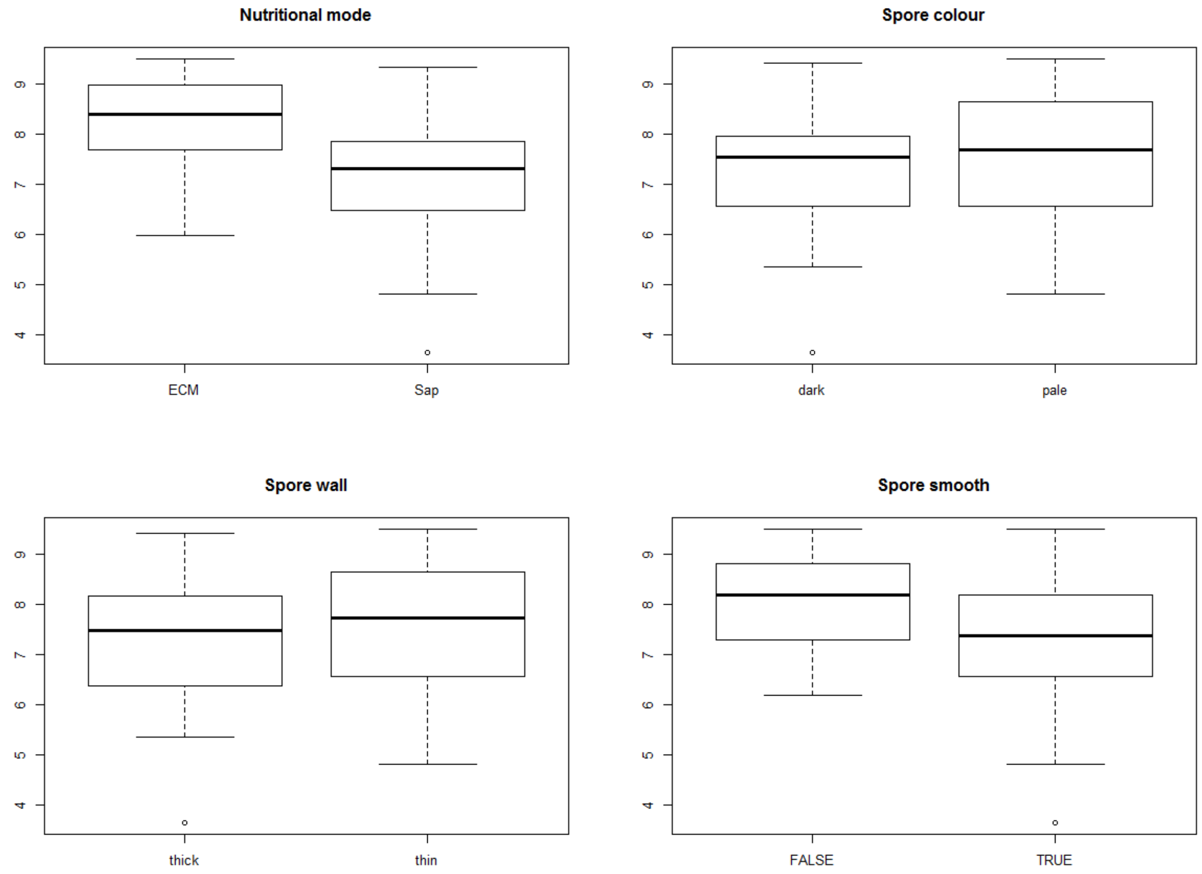

Figure S1.2. Continuous variable is Cap area.

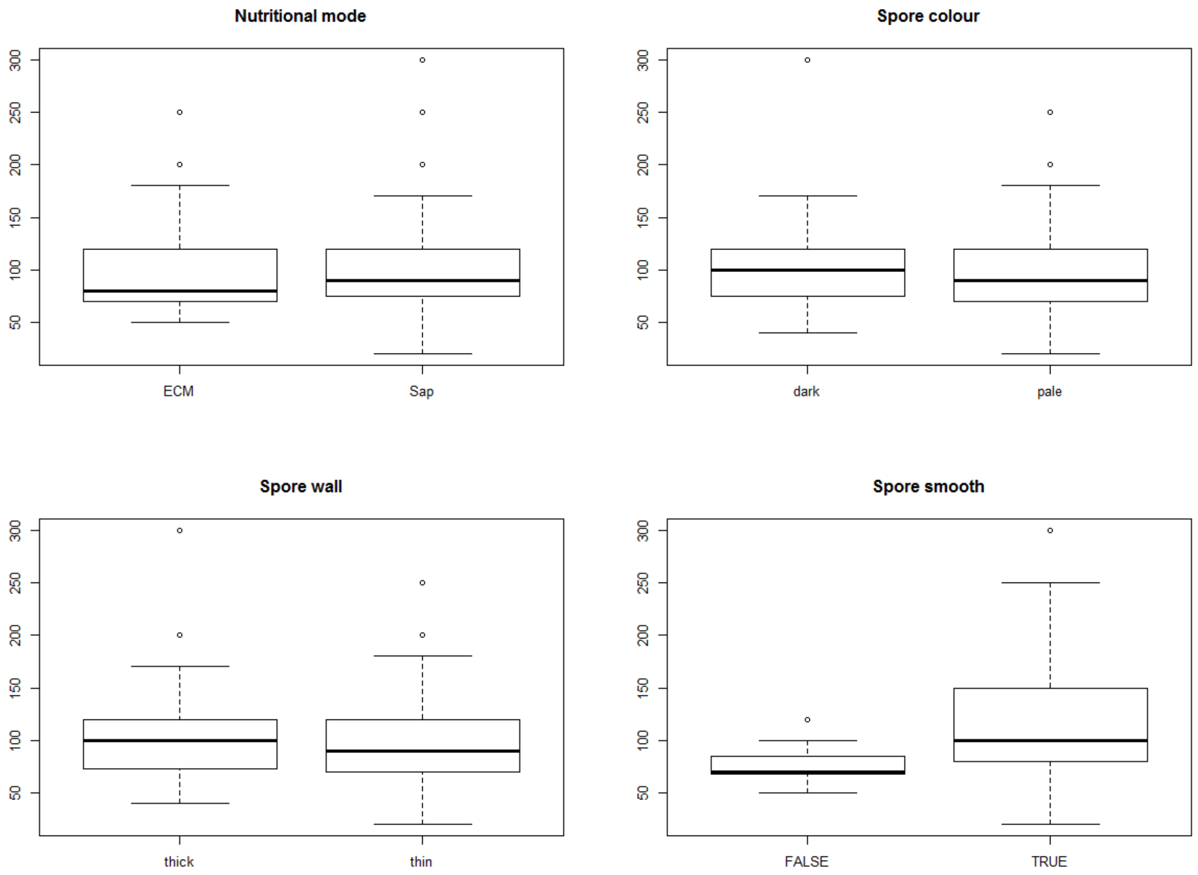

Figure S1.3. Continuous variable is Stipe height.

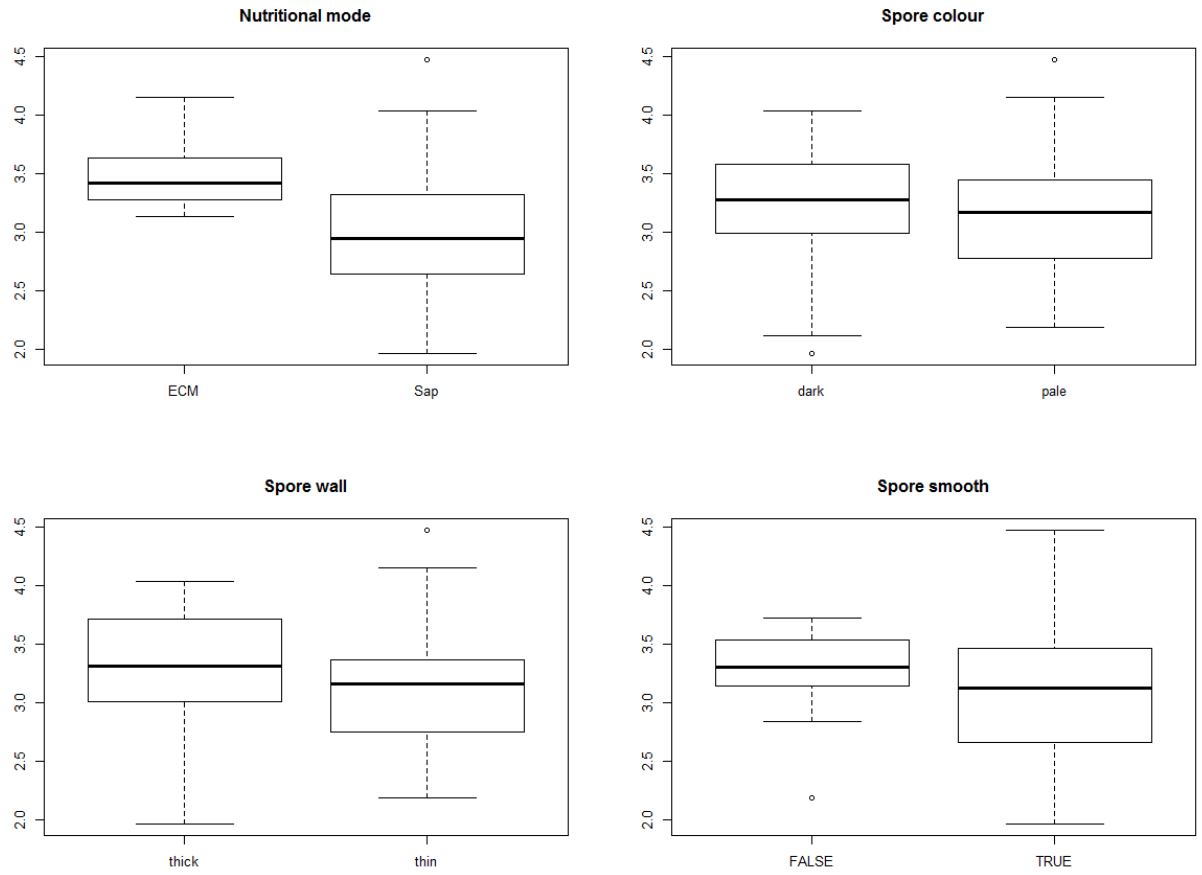

Figure S1.4. Continuous variable is Spore volume

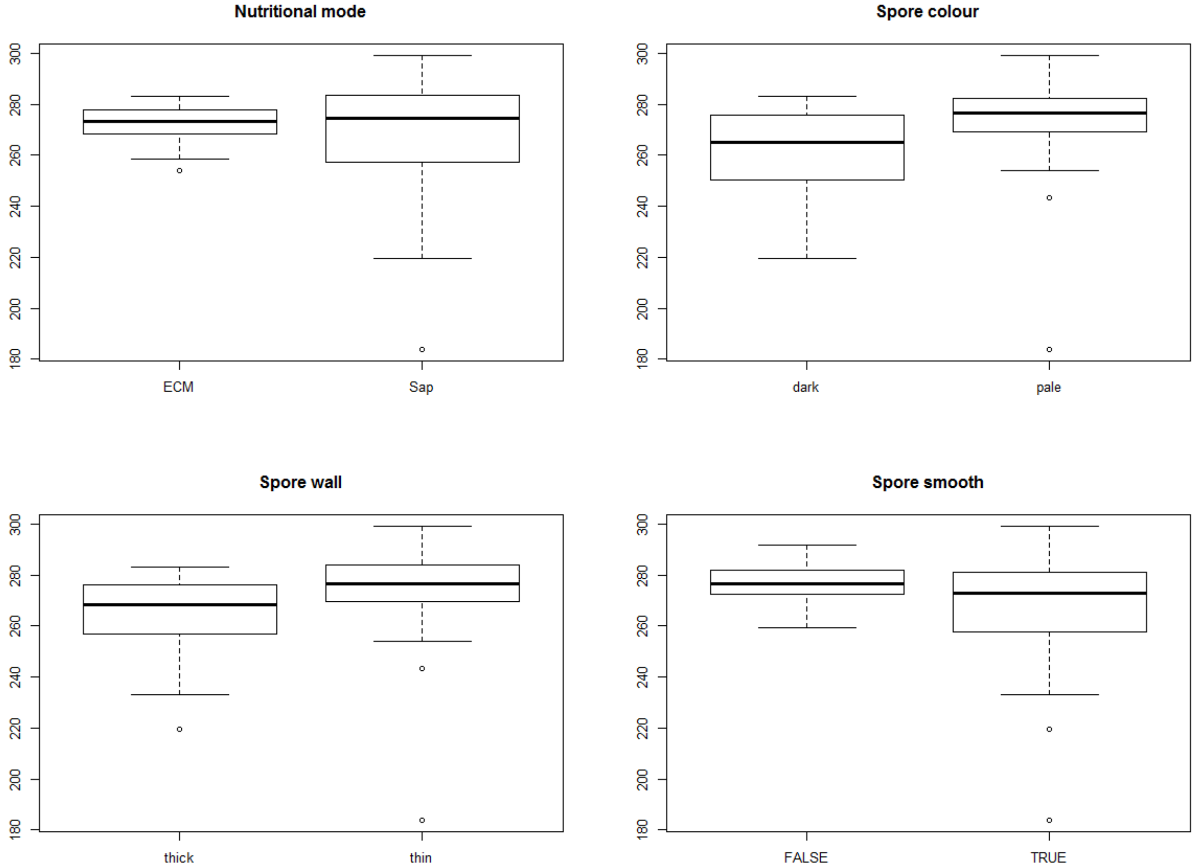

Fig. S1.5. Continuous variable is mean Fruiting day.

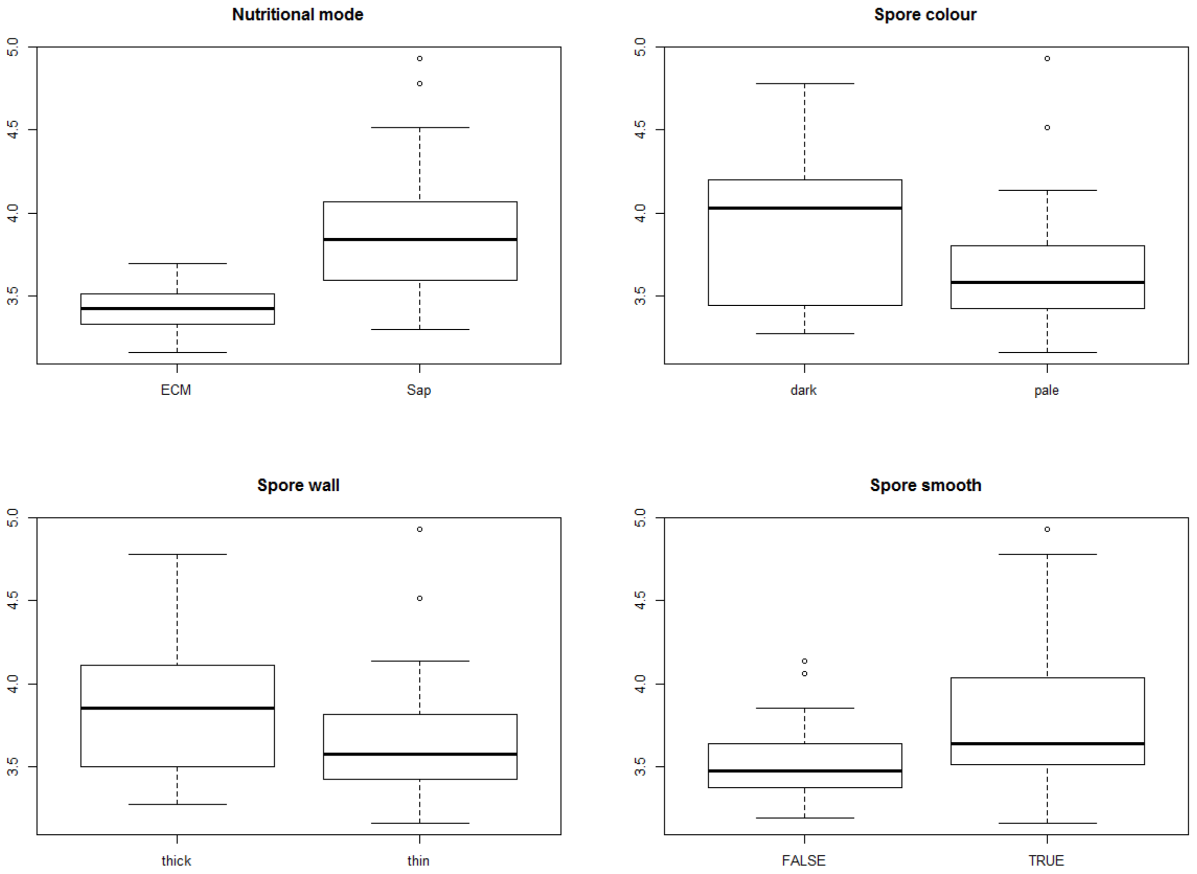

Figure S1.5. Continuous variable is standard deviation fruiting day.

	No traits		Nutri		Caparea		Stipe		Spore_ V		Sp_pale		Sp_smo		Sp_Wall		Fruit_M		Fruit_sd	
	Low	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low	High
Intercept	0.543	0.705	0.511	0.691	0.542	0.706	0.542	0.706	0.542	0.706	0.522	0.707	0.499	0.688	0.523	0.700	0.542	0.706	0.543	0.706
Latitude (1)	-0.073	0.104	-0.082	0.120	-0.073	0.104	-0.073	0.103	-0.074	0.103	-0.115	0.093	-0.120	0.093	-0.124	0.074	-0.073	0.104	-0.073	0.103
Time (2)	-0.123	-0.065	-0.157	-0.074	-0.123	-0.065	-0.123	-0.065	-0.122	-0.065	-0.157	-0.067	-0.151	-0.056	-0.150	-0.068	-0.123	-0.065	-0.123	-0.065
Lati:Time (4)	-0.002	0.029	0.025	0.071	-0.002	0.028	-0.002	0.029	-0.002	0.029	-0.019	0.038	0.031	0.085	-0.011	0.039	-0.002	0.029	-0.002	0.028
Trait (3)			-0.022	0.094	-0.032	0.023	-0.022	0.034	-0.020	0.036	-0.047	0.075	-0.022	0.105	-0.037	0.077	-0.038	0.015	-0.029	0.026
Latitude:Trait (5)			-0.082	0.067	-0.014	0.056	-0.014	0.056	-0.034	0.038	-0.041	0.114	-0.042	0.120	-0.008	0.136	-0.044	0.025	-0.059	0.011
Time:Trait (6)			-0.014	0.079	-0.024	0.020	-0.036	0.008	-0.035	0.009	-0.023	0.075	-0.038	0.064	-0.022	0.070	-0.010	0.033	-0.009	0.035
Lati:Time:Trait (7)			-0.082	-0.025	0.003	0.032	-0.009	0.021	-0.007	0.023	-0.029	0.039	-0.092	-0.029	-0.032	0.031	-0.015	0.016	-0.029	0.001
Intercept	0.564	0.714	0.536	0.703	0.564	0.713	0.566	0.712	0.564	0.713	0.539	0.711	0.528	0.701	0.540	0.705	0.564	0.713	0.564	0.713
Temp	-0.074	0.020	-0.103	0.021	-0.075	0.021	-0.075	0.021	-0.075	0.021	-0.068	0.062	-0.073	0.062	-0.053	0.067	-0.075	0.021	-0.074	0.020
Time	-0.122	-0.059	-0.160	-0.069	-0.122	-0.059	-0.123	-0.059	-0.122	-0.059	-0.162	-0.065	-0.167	-0.065	-0.158	-0.070	-0.122	-0.059	-0.122	-0.059
Temp:Time	-0.015	0.016	-0.045	0.004	-0.015	0.016	-0.015	0.016	-0.015	0.016	-0.021	0.035	-0.062	-0.007	-0.020	0.030	-0.015	0.016	-0.015	0.016
Trait			-0.029	0.087	-0.029	0.026	-0.022	0.033	-0.023	0.034	-0.043	0.081	-0.030	0.096	-0.032	0.083	-0.034	0.020	-0.035	0.021
Temp:Trait			-0.039	0.082	-0.045	0.012	-0.039	0.018	-0.027	0.030	-0.097	0.028	-0.093	0.036	-0.113	0.003	-0.027	0.028	-0.001	0.054
Time:Trait			-0.014	0.087	-0.024	0.023	-0.034	0.014	-0.039	0.009	-0.020	0.084	-0.020	0.088	-0.011	0.086	-0.014	0.032	-0.015	0.033
Temp:Time:Trait			0.002	0.062	-0.030	-0.002	-0.019	0.011	-0.015	0.015	-0.042	0.023	0.016	0.079	-0.038	0.024	-0.020	0.009	-0.002	0.027
Intercept	0.514	0.649	0.496	0.648	0.515	0.649	0.514	0.649	0.515	0.649	0.497	0.652	0.479	0.636	0.498	0.648	0.514	0.649	0.514	0.649
Rain	-0.018	0.081	-0.035	0.122	-0.017	0.081	-0.018	0.081	-0.018	0.082	-0.114	0.050	-0.088	0.089	-0.107	0.040	-0.017	0.080	-0.016	0.078
Time	-0.129	-0.073	-0.169	-0.090	-0.129	-0.073	-0.129	-0.073	-0.129	-0.073	-0.149	-0.063	-0.158	-0.068	-0.145	-0.066	-0.129	-0.073	-0.128	-0.074
Rain:Time	-0.026	0.000	-0.027	0.013	-0.026	0.000	-0.026	0.000	-0.026	0.000	-0.032	0.014	-0.018	0.028	-0.031	0.010	-0.026	0.000	-0.025	0.001
Trait			-0.037	0.068	-0.029	0.021	-0.020	0.030	-0.017	0.034	-0.044	0.066	-0.024	0.089	-0.038	0.067	-0.035	0.013	-0.031	0.018
Rain:Trait			-0.111	0.075	-0.019	0.067	-0.040	0.048	-0.046	0.043	-0.004	0.184	-0.057	0.142	0.016	0.192	-0.001	0.081	-0.106	-0.025
Time:Trait			0.000	0.086	-0.031	0.011	-0.034	0.007	-0.034	0.008	-0.039	0.053	-0.032	0.063	-0.037	0.050	-0.021	0.020	0.009	0.049
Rain:Time:Trait			-0.034	0.016	-0.017	0.007	-0.011	0.013	-0.004	0.020	-0.032	0.022	-0.051	0.002	-0.029	0.021	-0.023	0.002	-0.005	0.019
Intercept	0.568	0.705	0.539	0.695	0.515	0.649	0.568	0.705	0.568	0.706	0.545	0.705	0.524	0.687	0.548	0.702	0.568	0.705	0.567	0.705
HT	-0.032	0.049	-0.067	0.059	-0.017	0.081	-0.031	0.049	-0.031	0.049	-0.107	0.026	-0.099	0.043	-0.098	0.021	-0.031	0.048	-0.032	0.046
Time	-0.131	-0.076	-0.162	-0.086	-0.129	-0.073	-0.131	-0.076	-0.131	-0.076	-0.144	-0.062	-0.153	-0.067	-0.140	-0.065	-0.131	-0.076	-0.129	-0.076
HT:Time	-0.036	-0.006	-0.041	0.005	-0.026	0.000	-0.037	-0.006	-0.036	-0.007	-0.033	0.017	-0.033	0.019	-0.030	0.014	-0.036	-0.007	-0.035	-0.006
Trait			-0.025	0.084	-0.029	0.021	-0.019	0.033	-0.021	0.032	-0.042	0.074	-0.017	0.101	-0.035	0.073	-0.031	0.020	-0.033	0.019
HT:Trait			-0.054	0.095	-0.019	0.067	-0.034	0.037	-0.040	0.032	-0.006	0.145	-0.030	0.130	0.004	0.148	0.006	0.072	-0.078	-0.010
Time:Trait			-0.009	0.072	-0.031	0.011	-0.032	0.007	-0.030	0.009	-0.043	0.043	-0.036	0.054	-0.042	0.040	-0.026	0.012	0.013	0.050
HT:Time:Trait			-0.032	0.022	-0.017	0.007	-0.014	0.012	-0.002	0.024	-0.047	0.010	-0.048	0.009	-0.048	0.004	-0.030	-0.006	0.004	0.029

Table S2. The 95 % credibility intervals of the coefficients associated with the different models. Each pair of columns gives the results from the model of the specific trait in interaction with latitude, climate and time. Numbers in brackets in the latitude section correspond to the effects depicted in Fig. 1, from (1) at the bottom to (7) at the top. This numbering also applies to the sections for Temp (temperature), Rain and HT (Hygrothermic Index). The lower four rows of each section are reproduced in the colour chart in Figure 3 of the main text.

Key to column headers: Nutri: Nutritional mode (ECM or saprotroph); Cap A: Cap area; Stipe: Maximum height of stipe; Sp pale: spore colour; Sp smo: spore smoothness; Sp wall: spore wall thickness; Fruit M: fruiting season mean; Fruit sd: fruiting season standard deviation (log).

The cap size is defined as the area of an average sized cap, and for the stipe height used the maximum height recorded. The average fruiting day is mean ordinal day, and the standard deviation of fruiting day describe the length of the fruiting season for the individual species.

```
###############

#Summary of analyses for nutritional mode using INLA for the full trait-specific model as presented in Gange et al. , Trait-dependent distributional shifts in fruiting of common British fungi

###############


#dag.df  = dataframe with the observational data

#y = number of records per species per VC per year

#qE = expected number of records per species per VC per Year

#Sp1 = as.numeric(dag.df$Sp)#index the different species

#N.sp = nlevels(dag.df$Sp) #number of species

#Sp2 = Sp1+N.sp #Index of species to identify additional random contributions associated with species, interaction species and Latitude

#Sp3 = Sp2+N.sp #Index of species to identify additional random contributions associated with species, interaction species and Time

#Sp4 = Sp3+N.sp #Index of species to identify additional random contributions associated with species, interaction species and Lat:Time

#Latitude = latitudinal desimal degree

#Time = year

#LatitudeTime = Latitude*Time

#VC = vice county number

#UK.adj = a list of neighbouring VC's
```

```
inla.Nutri <- Inla(y~offset(log(qE))+

        f(Sp1,model="iid")+f(Sp2,Latitude,model="iid")+f(Sp3,Time,model="iid")+f(Sp4,LatitudeTime,model="iid")+

        f(VC,model="bym",graph=UK.adj)+f(Time,model="iid")+Latitude*Time*Nutri,

        family="nbinomial",control.compute=list(waic=T),data=dag.df)


summary(inla.Nutri)
```

```
Call:

  c("inla(formula = y ~ offset(log(qE)) + f(Sp1, ",  "    model = \"iid\") + f(Sp2, Latitude,
model = \"iid\") +     f(Sp3, Time, ",  "    model = \"iid\") + f(Sp4, LatitudeTime, model =
\"iid\") + f(VC, model = \"bym\", ",  "    graph = UK.adj) +     f(Time, model = \"iid\") +
Latitude * Time * ",  "    Nutri, family = \"nbinomial\", data = dag.df, control.compute =
list(waic = T))" )


Time used:

  Pre-processing    Running inla Post-processing           Total

1.5906      75579.0516          7.5242      75588.1665
```

```
Fixed effects:
                        mean     sd    0.025quant 0.5quant 0.975quant    mode   kld
(Intercept)             0.6012 0.0462     0.5104   0.6012     0.6920      0.6012   0
Latitude                0.0196 0.0520    -0.0829   0.0198     0.1213      0.0201   0
Time                   -0.1153 0.0215    -0.1576  -0.1153    -0.0731     -0.1154   0
Nutrisap                0.0360 0.0296    -0.0223   0.0360     0.0942      0.0360   0
Latitude:Time           0.0477 0.0118     0.0245   0.0477     0.0708      0.0477   0
Latitude:Nutrisap      -0.0070 0.0382    -0.0824  -0.0069     0.0683     -0.0069   0
Time:Nutrisap           0.0326 0.0239    -0.0145   0.0326     0.0798      0.0326   0
Latitude:Time:Nutrisap -0.0539 0.0146    -0.0827  -0.0540    -0.0251     -0.0540   0

Random effects:
  Name    Model
Sp1   IID model
Sp2   IID model
Sp3   IID model
Sp4   IID model
VC   BYM model
Time   IID model

Model hyperparameters:
                                      mean     sd    0.025quant 0.5quant 0.975quant    mode
size for the nbinomial observations   5.43   0.0642      5.303    5.430      5.556     5.431
Precision for Sp2                    52.07  10.4329     32.691   51.913     73.084    52.460
Precision for Sp1                    89.33  17.2561     57.630   88.858    124.781    88.962
Precision for Sp3                   141.29  28.6123     94.227  138.121    206.168   131.816
Precision for Sp4                   471.08 118.5723    284.721  455.161    747.564   424.411
Precision for VC (iid component)     10.03   2.2620      6.229    9.813     15.079     9.420
Precision for VC (spatial component) 16.42  12.4821      4.283   12.873     49.455     8.583
Precision for Time                  211.03  52.8077    120.903  206.975    326.282   200.250

Expected number of effective parameters(std dev): 368.33(2.982)
Number of equivalent replicates : 192.10
```

```
Watanabe-Akaike information criterion (WAIC) ...: 306946.32

Effective number of parameters .................: 401.01


Marginal log-Likelihood:  -153970.39

Posterior marginals for linear predictor and fitted values computed
```

Figure S1

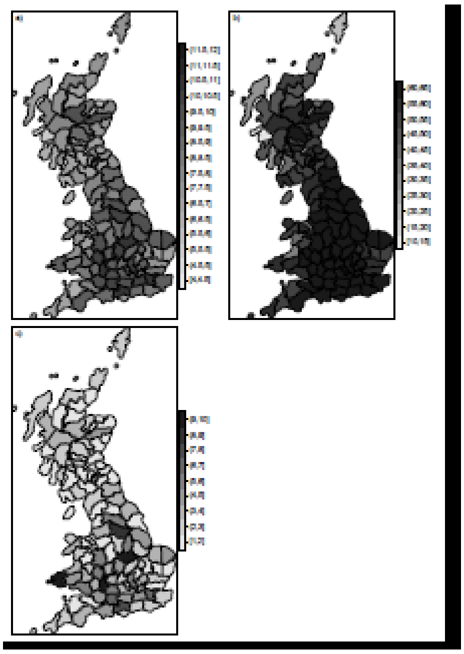

Figure S2