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Please cite this publication as follows:

Heegaard, E., Boddy, L., Diez, J. M., Halvorsen, R., Kauserud, H., Kuijper, T., ... Egli, S. (2017). Fine-scale spatiotemporal dynamics of fungal fruiting: Prevalence, amplitude, range and continuity. *Ecography*, 40(8), 947-959 .
<https://doi.org/10.1111/ecog.02256>

Fine-scale spatiotemporal dynamics of fungal fruiting: prevalence, amplitude, range and continuity

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Despite the critical importance of fungi as symbionts with plants, resources for animals, and drivers of ecosystem function, the spatiotemporal distributions of fungi remain poorly understood. The belowground life cycle of fungi makes it difficult to assess spatial patterns and dynamic processes even with recent molecular techniques. Here we offer an explicit spatiotemporal Bayesian inference of the drivers behind spatial distributions from investigation of a Swiss inventory of fungal fruit bodies. The unique inventory includes three temperate forest sites in which a total of 73 952 fungal fruit bodies were recorded systematically in a spatially explicit design between 1992 and 2006.

Our motivation is to understand how broad-scale climate factors may influence spatiotemporal dynamics of fungal fruiting within forests, and if any such effects vary between two functional groups, ectomycorrhizal (ECM) and saprotrophic fungi. For both groups we asked: 1) how consistent are the locations of fruiting patches, the sizes of patches, the quantities of fruit bodies, and of prevalence (occupancy)? 2) Do the annual spatial characteristics of fungal fruiting change systematically over time? 3) Are spatial characteristics of fungal fruiting driven by climatic variation?

We found high inter-annual continuity in fruiting for both functional groups. The saprotrophic species were characterised by small patches with variable fruit body counts. In contrast, ECM species were present in larger, but more distinctly delimited patches. The spatial characteristics of the fungal community were only indirectly influenced by climate. However, climate variability influenced overall yields and prevalence, which again links to spatial structure of fruit bodies. Both yield and prevalence were correlated with the amplitudes of occurrence and of fruit body counts, but only prevalence influenced the spatial range. Summarizing, climatic variability affects forest-stand fungal distributions via its influence on yield (amount) and prevalence (occupancy), whereas fungal life-history strategies dictate fine-scale spatial characteristics.

The spatial and temporal distribution patterns of forest fungi remain poorly understood, largely because fungi spend most of their time hidden below ground or within other substrates. Even though the popularity of molecular approaches for recording presence of fungi in the soil is increasing (Lindahl et al. 2013), censuses of aboveground fruit bodies remain a useful tool for investigating fungal distributions, on both coarse and fine scales (Wollan et al. 2008, Büntgen et al. 2013). If sampling effort is sufficient, fruit bodies can provide important quantitative information about the spatial and temporal distribution of fungal species, but the requirement for systematic sampling makes spatial patterns of fungal production hard to quantify. Nevertheless, the potential reward for new insights into the spatial patterns of fungal fruiting is high. Fruiting is a basic

biological process of many fungi, and fruit body production is an important part of ecosystems and food webs (Maser et al. 1978, Komonen 2003, Schigel 2011, Komonen et al. 2012), with groups of organisms that depend on fungal fruit bodies for food and/or habitat, such as insects, mammals, slugs and snails (Wheeler and Blackwell 1984, Worthen 1988, Claridge and May 1994, Yamashita and Hijii 2007). Several studies have shown that the timing of fungal fruiting can be driven by climatic variability at local (Sato et al. 2012, Büntgen et al. 2013, Ágreda et al. 2015), regional (Gange et al. 2007, Diez et al. 2013), and national (Kauserud et al. 2008, 2010, 2012) scales. Given these climatic controls over yield and timing of fruit body production, it is also possible that climate may affect spatial patterns of fruit body production, and these changes in

spatial patterns could have important implications for the distributions of ecosystem functions and resources.

The spatial distribution of fungi in a forest depends on several key factors associated with local distribution of suitable substrates, with life-history strategies including their capacity for dispersal, trade-offs between growth and reproduction, acquisition strategy for energy and nutrients, and biological interactions such as competition (Dix and Webster 1995). Dispersal is difficult to quantify, but most fruit bodies are ephemeral and produce millions of microscopic spores with the potential for long-distance spread via air currents (Ingold 1971, Hallenberg and Kúffer 2001). Nonetheless, most spores are deposited within a few metres of the fruit body (Stenlid 2008, Galante et al. 2011, Norros et al. 2012), and thereby contribute to fine-scale viability of the populations. Such local mass deposition may compensate for the low probability that a single spore will germinate and establish a new mycelium. The masses of spores dispersed across shorter distances point to the importance of deposition rates across the forest floor as well as for local environmental conditions to play a central part in the shaping of the fine-scaled spatial pattern of fungal mycelia and fungal community dynamics (Andrew et al. 2016). However, production of fungal fruit bodies only takes place if established mycelia have successfully mated and captured sufficient nutritional resources.

Much can be learned about the processes driving fungal distributions by comparing functional groups because the distribution of suitable substrates and mode of resource acquisition differs strongly between the two major functional groups of soil-dwelling basidiomycetes: ectomycorrhizal (ECM) and saprotrophic species. Most fungal ecologists treat saprotrophic and biotrophic members (ECM, pathogens) as separate communities according to their trophic level. This within-trophic-level approach is commonly used because at a single trophic level resource acquisition is similar (Koide 2012). The ECM species are largely dependent on an association with plant roots for carbon nutrition, so the spread, distribution and vitality of suitable plant hosts is expected to influence spatial patterns of ECM fruiting (Pestaña and Santolamazza-Carbone 2010). In contrast, the distribution of saprotrophic species is coupled to the distribution of the dead organic material that they decompose to access carbon and mineral nutrients (Boddy et al. 2007). Both groups acquire resources for mycelial growth and for fruit body production. It is likely that there is a classic trade-off between sexual reproduction and mycelial growth in both groups (Deacon and Fleming 1992, Gardes and Bruns 1996), and fruiting may be intimately tied to the longevity and consistency of specific resource availabilities.

Fungal individuals can also vary from short-lived mycelia (Gryta et al. 1997, Guidot et al. 2004) to genets of considerable age (Ferguson et al. 2003, Smith and Read 2008). For most saprotrophic species resources consist of patches of organic substrates that will be depleted unless replenished by new inputs such as litter, branch or tree fall (Boddy et al. 2007). Upon resource depletion, saprotrophic species may move to nearby resources by mycelial growth and/or spore dispersal via fruit bodies. The reliance on resources

with a relatively short 'life span' suggests that saprotrophs may employ strategies in which fruiting reflects fine-scaled patchiness and rapid temporal dynamics. Furthermore, such strategies may result in low prevalence of most species within a given locality. In contrast, ECM species' reliance on one or more host plants (Simard et al. 1997, Beiler et al. 2010, Egli et al. 2010) suggests that longevity and fruiting may depend more on host conditions (Högberg et al. 1999, Högberg and Read 2006, Leski et al. 2010) and, perhaps, on competition with other fungi (Kennedy et al. 2007, 2009, Kennedy 2010). Indeed, recent studies have suggested a relationship between mushroom production and tree growth (Büntgen et al. 2012, 2013, 2015), and almost a complete cessation of ECM fungal production following experimental tree girdling (Högberg et al. 2001). Both ECM and saprotrophic species show considerable variation in the timing of fruiting, in the extent of patches with fruiting fungi and in the size of mycelial genets. The latter may vary from less than a few centimetres across (Gryta et al. 1997, Fiore-Donno and Martin 2001, Riviere et al. 2006, Murat et al. 2013), to individuals covering several hundred square metres or even hectares (Dahlberg and Stenlid 1994, Bonello et al. 1998, Boddy et al. 2007, Douhan et al. 2011). Population genetic analyses of fruit bodies have revealed genets ranging from a few meters to 65 m and beyond (Kretzer et al. 2005, Bergemann et al. 2006, Carriconde et al. 2008a, b, Burchhardt et al. 2011). Such variability is also reflected by community analyses among ECM species, where patches of relatively homogeneous community composition usually are smaller than 3 m across, but occasionally much larger (Tedersoo et al. 2003, Lilleskov et al. 2004, Luis et al. 2005).

In this study, we used a unique 15-yr dataset from a Swiss temperate forest to investigate how the spatiotemporal dynamics of fungal fruiting is related to fungal life history, climatic conditions and total annual fruit body production. This dataset (for further description, see Egli (2011), Büntgen et al. (2013)) consists of weekly fruit body counts made during the season (week 21 to 52) between 1992 and 2006 within three 300 m² plots, each divided into 1 m² sub-subplots. A total of 73 952 fruit bodies were recorded from 126 saprotrophic species and 178 ECM species. Our main focus is a comparison of temporal dynamics of spatial patterns of the two functional groups, ECM versus saprotrophic fungi, by assessment of the following key questions: 1) how is the fine-scale spatiotemporal distribution of fungal fruit bodies characterised with respect to temporal continuity, spatial patch size, amplitude of fruiting, and prevalence (commonness); 2) do the annual spatial characteristics of fungal fruiting change systematically over time; and 3) are the annual spatial characteristics of fungal fruiting driven by climatic variation and/or annual yield and do they differ among functional groups? To characterise the spatiotemporal patterns we developed latent Gaussian field (GF) models, combining a temporal autoregressive process and Matérn covariance (Rue et al. 2009, Lindgren et al. 2011). Importantly, these models have parameters with relevant biological interpretations, allowing us to directly test how fungal fruit body patch sizes and spatial prevalence are related to climate and fungal life history.

Material and methods

Study area

The study was carried out in three long-term research plots, 30 × 10 m each, situated in the La Chanéaz forest, Switzerland (46°48'03"N and 07°00'11"E (Egli et al. 2006, Egli 2011, Büntgen et al. 2013)), which is a 75 ha nature reserve established in 1975. The woodland includes *Fagus sylvatica*, *Picea abies*, *Abies alba*, *Pinus silvestris*, *Pinus strobus*, and *Larix decidua*, and is situated just below 600 m a.s.l. The annual precipitation of the area is 845 mm, and the annual mean temperature is 8.5°C (1961–1990 normal of the Payerne climate station (46°87'42"N and 06°56'33"E). Fungal fruit bodies were monitored in all plots weekly from week 21 to week 52 every year from 1975 to 2006. A fruit body was recorded when first observed and then colour stained to avoid repeated counting in subsequent weeks. From 1992 until 2006 the three plots were divided into three contiguous subplots (10 × 10 m), each of which were further gridded into 100 sub-subplots, 1 × 1 m. Records of fruit bodies are thus available for a total of 300 sub-subplots in each plot, i.e. with a spatial resolution of 1 m, a temporal resolution of 1 week (weeks 21–52), and a temporal extent of 15 yr.

Data

Only records of species of Agaricomycetes producing annual 'agaricoid' basidiocarps were included in the study, while species producing perennial fruit bodies (typically polypores) or fruiting more erratically (e.g. jelly fungi) were omitted. The species list (Supplementary material Appendix 1, Table A1), was split into two functional groups: saprotrophic and ECM species. A strict definition was applied to the categorization, although we recognize that there are uncertainties about the position of some taxa (Knudsen and Vesterholt 2012). The annual number of fruit bodies appearing in each sub-subplot was obtained separately for each functional group. For each functional group two sub-subplot specific response variables, four in total, were derived to be used in the analyses: 1) presence-absence of fruit bodies of each group, and 2) number of fruit bodies belonging to each group (abundance). The spatial coordinates for these response variables were given by the position of the sub-subplot within the rectangular research plot (30 × 10 m), and the temporal covariate was represented by the year. Separately for every plot and functional group these data were used to estimate the spatial and temporal characteristics of fungal fruiting.

The spatiotemporal fruiting patterns were analysed with respect to the following covariates: climate, represented by annual mean temperature (9.6 C ± 0.5 SD) and total annual precipitation (882 mm ± 147 SD), obtained from the weather station Payerne 7 km from the study plots (source: MeteoSchweiz); functional group (ECM or saprotrophic); yield (annual sum of fruit bodies for each functional group per plot); and year. We used annual climatic data to match the annual resolution of the response variables, i.e. presence-absence and number of fruit bodies. All covariates were scaled to zero mean and unit variance.

Statistical approach

The general analytical aim of this study was to identify and specify latent spatial patterns as Gaussian field and assess the biological processes hidden in the characterisation of the latent patterns (Wiegand et al. 2003). The three plots were analysed separately in Bayesian hierarchical models by integrated nested laplace approximations, INLA (Rue et al. 2009). For each plot, species group and response type we performed two main analyses: A) estimating the posterior distribution of the full space-time characteristics (Lindgren et al. 2011, Cameletti et al. 2013, Cosandey-Godin et al. 2014) across the entire 15-yr period; and B) estimating the spatial characteristics (Blangiardo and Cameletti 2015) of fruit body production separately for each year. The central element of the models estimated through A) and B) was the Gaussian field (GF), which provided spatial and temporal hyper-parameters. These hyper-parameters for fungal fruiting can be interpreted as patch size (range), amplitude of fruiting pattern (field variance), and continuity across years (temporal autocorrelation, AR1). In addition to the time-space parameters, an estimate of the probability of absence (zero-probability = 1 – prevalence) was obtained from the distribution of fruit body counts.

From the annual spatial analyses B) two new datasets were assembled, one with results using presence-absence data and one using numbers of fruit bodies. Each of these datasets contained the expectation and variance of the marginal posterior distribution on a logarithmic (base = 2) scale for each spatial parameter, for both functional groups, all 15 yr and the 3 plots. These two datasets were analysed by linear mixed-effect models (Pinheiro and Bates 2000). For each spatial characteristic the expectation was considered as the response, with the variance as a weight. The sensitivity of the spatial parameters was then estimated as fixed effects of climate, nutritional mode, yield, and the other spatial characteristics. The other spatial characteristics were included to assess the degree of co-variation of spatial characteristics between time-points. In addition, a plot-specific random contribution was included accounting for differences between the plots. The fixed effects were evaluated by backward elimination from a full model including all two-way interactions. All calculations were performed using R, ver. 3.1.1 (R Core Team), and the main packages were INLA, <www.r-inla.org/>, (Rue et al. 2009), nlme (Pinheiro and Bates 2000).

Space-time model specification

For the Bayesian inference we applied a Gaussian latent model, which implies a Gaussian prior for all parameters of the linear predictor (η) (Rue et al. 2009, Lindgren et al. 2011). The response (y_{it}) for the i 'th spatial location ($i = 1, \dots, 300$) at time t ($t = 1, \dots, 14, 15$) was either presence-absence (Bernoulli likelihood) or fruit body counts (zero-inflated Poisson likelihood):

$$y_{it} | \theta, x_{it} \sim P(y_{it} | \mu_{it}, \phi)$$

where x_{it} is a Gaussian field (GF) and θ contains the parameters and hyper-parameters of the model ($\beta, \phi, \alpha, \sigma_w^2, \kappa$); β is a fixed intercept, ϕ is the additional hyper-parameter of

the zero-inflated model describing the expected probability of empty sub-subplot (pzero), α is the temporal correlation defined as an autoregressive order – 1 process, σ_w^2 is the variance of the Gaussian field, and κ as the scale parameter for the Matérn spatial correlation, hence the two likelihoods as applied here are:

$$P(y_{it} | \mu_{it}) = \mu_{it}^{y_{it}} (1 - \mu_{it})^{1 - y_{it}}$$

$$P(y_{it} | \mu_{it}, \phi) = \phi \times 1_{y_{it}=0} + (1 - \phi) \times \text{Poisson}(y_{it} | \mu_{it}, y_{it} > 0)$$

The mean (μ_{it}) parameter of the likelihood is connected to the linear predictor (η_{it}) by a link function $g(\cdot)$:

$$g(\mu_{it}) = \eta_{it}$$

$$\eta_{it} = \beta_0 + x_{it}$$

$$x_{it} = \alpha x_{it-1} + w_{it}$$

$$w_{it} \sim N(0, \sigma_w^2 R(\kappa, v))$$

$$x \sim \text{GF}(0, Q^{-1})$$

where x is the Gaussian field (GF) with zero mean and precision matrix Q (inverse covariance $\Sigma = Q^{-1}$). The GF (x_{it}) contains an autoregressive contribution (αx_{it-1}) and a spatial contribution (w_{it}). Here, the spatial contribution is a spatial GF with zero mean and covariance; $w_{it} \sim N(0, \sigma_w^2 R(\kappa, v)) = N(0, Q_S^{-1})$, where σ_w^2 is the field variance, i.e. the fluctuation of the field, and $R(\kappa, v)$ is a Matérn correlation specified by the parameters κ = scale and v = smoothness:

$$R(h, \kappa, v) = \frac{2^{1-v}}{\Gamma(v)} (\kappa h)^v K_v(\kappa h)$$

where h is the Euclidean distance and K_v is a modified Bessel function of the second kind. Smoothness is often treated as constant (here $v = 1$). The temporal and spatial contributions provide precision matrices Q_T and Q_S , respectively, which were combined by the Kronecker product that keeps their contributions independent; $Q = Q_T \otimes Q_S$.

The temporal correlation fulfils assumptions of conditional independence, meaning that a sparse tri-diagonal precision is produced by each time-point only being connected to adjacent time-points (Cameletti et al. 2013, Blangiardo and Cameletti 2015). In comparison, the spatial Gaussian field (GF) supports a dense covariance matrix, i.e. with all points in space connected directly. To simplify computations, a sparse precision matrix was looked for as a substitute for the spatial GF, i.e. a Gaussian Markov random field, GMRF (Rue and Held 2005). This was obtained by a stochastic partial differentiation equation, SPDE (Lindgren et al. 2011), by which a representation of the GF was found through a linear combination of basis functions and Gaussian weights that are both defined on a mesh covering the study domain (Fig. 1a). A basis function, piecewise linear, is defined for every vertex, i.e. with 1 at the vertex and 0 at other vertices, and with weights that are the height of the GMRF at the vertex, with points in between vertices being a weighted average of neighbouring vertices. Hence, the representation is Markovian, and the now sparse precision matrix (Q_S) of the weights (GMRF) is provided as a function of parameters of the Matérn correlation (Lindgren et al. 2011). Finally, the sparse matrices of both temporal and spatial precision allow the Bayesian inference to be provided through the integrated nested Laplace approximation, INLA (Rue et al. 2009, Lindgren et al. 2011), a fast alternative to MCMC algorithms. The analyses were performed on A) a full space-time model and B) individual spatial models for each year. The analysis for each individual year, i.e. spatial GF, followed the same outline, but without the temporal contribution to the precision. The precision matrix then becomes: $Q = 1 \otimes Q_S$, which only includes the field variance and the Matérn correlation.

Parameters of interest

In this study we were primarily interested in the posterior distributions of the hyper-parameters specifying the

Figure 1. (a) The field design by regular 1 by 1 m adjacent sub-subplots (red), and the grid (mesh) upon which the GMRF is produced. Note that we include vertices outside the study domain to handle edge effects. The triangulation ties the vertices together. A stochastic partial differentiation equation approach provides a sparse precision matrix representation which is used to estimate (b) the posterior distribution of the hyper-parameters range and field variance, which provide the spatial characteristics that are used to predict the spatial pattern at link scale (c). Note that random fields with similar range and field variance may produce different realizations so that these parameters are just descriptors of spatial characteristics.

temporal and spatial characteristics of the GF. We, therefore, focused on α = temporal correlation, and the Matérn covariance by κ = scale parameter and τ = local precision. From the latter two hyper-parameters we obtained the range ($\rho = (\sqrt{8\nu})\kappa^{-1}$, Fig. 1b), i.e. the distance at which the correlation was reduced to 0.1, and the field variance ($\sigma_w^2 = (4\pi\tau^2\kappa^2)^{-1}$, Fig. 1b), which combine into a spatial Gaussian Markov random field (Fig. 1c). These parameters (α , ρ and σ_w^2) combined with the distributional parameter (ϕ) translate into the time-spatial characteristics of fruit body production. The continuity (α = temporal correlation) describes the extent to which next year is expected to be a repetition of the previous year, i.e. the degree to which the signal continues from year to year. The patch size (ρ = range) describes the spatial distance at which the correlation between sub-subplots is reduced to a certain level (here $\rho \sim 0.1$). A larger range indicates wider patches of occurrences or more similar fruit body counts across larger distance. The fruiting amplitude (σ_w^2 = field variance) describes the variation of the values taken by the field across all sub-subplots, i.e. a low field variance has little variation in link-transformed expected fruit body production across the sub-subplots whereas a high field variance suggests a higher amplitude of values across the field. A high field variance may be thought of as a rough sea, whereas a low field variance may be understood as a calm ocean. Finally the zero-probability (ϕ = p_{zero}) describes the relative number of sub-subplots not occupied by any fruit bodies. This is the complement of the prevalence, i.e. the probability of sub-subplots being occupied.

Results

Spatiotemporal trends in fungal fruiting

The spatiotemporal model shows the average spatial and temporal characteristics in the 15-yr study period (Fig. 2). The ranges of ECM species' presence-absence exceeded 10 m (Fig. 2a, red lines), whereas for saprotrophic species (blue lines) ranges less than 10 m were found. For fruit body counts (Fig. 2d) the ranges were mainly between 3 and 5 m for ECM and less than 3 m for saprotrophic species.

The expected field variance was higher for ECM species' presence-absence in plots 54 and 59 (Fig. 2b), indicating a relatively larger difference between high- and low-probability areas within these plots than observed for the saprotrophic species. For the number of fruit bodies, a contrasting pattern was found with higher field variance for saprotrophic species (Fig. 2e). This suggests that saprotrophic species are more variable in the relative amount of fruit bodies produced per unit area than the ECM species.

With respect to continuity, or temporal correlation of fruit body production, no clear difference between the two functional groups was found. For fruit body presence-absence data, the continuity between years was generally high both for saprotrophic and ECM species ($AR1 > 0.6$, Fig. 2c) while, as expected, the continuity was lower for count data (Fig. 2f).

The zero probability, and hence, the prevalence, varied strongly among plots and differed between functional groups (Fig. 2g).

Temporal trends in spatial fruiting characteristics

In total, 180 and 270 posterior distributions were obtained for the parameters related to the spatial distributions of each of presence-absence and fruit body counts (Supplementary material Appendix 1, Fig. A2–A4). These were used to assess the temporal variation in annual spatial characteristics of fruiting during the study period 1992–2006.

For presence-absence of fruit bodies the expected range varied strongly, from 3 to 30 m, throughout the 15 yr (Fig. 3a). The range showed no temporal trend ($p = 0.839$), but the mean range differed significantly between ECM and saprotrophic species (9.8 and 6.1 m, respectively; $p < 0.001$, Fig. 3a). The annual ranges of the number of fruit bodies produced did not differ between the functional groups, and no significant temporal trend was observed over the 15 yr ($p = 0.345$ and 0.239 , respectively, Fig. 3c).

There was slightly higher field variance for ECM than for saprotrophic species' presence-absence during the 15 yr, but the considerable inter-annual variability of the field variance observed for saprotrophic species made the difference between functional groups borderline significant only (p -value = 0.096 , Fig. 3b). The fruit body count analyses, on the other hand, revealed a significantly larger field variance for saprotrophic species than for ECM species ($p < 0.001$, Fig. 3d), but the temporal trend ($p < 0.001$) did not differ significantly between the functional groups ($p = 0.595$).

Interestingly, the zero probability derived from the fruit body count model showed a temporal decline in number of occupied sub-subplots, stronger for ECM than for saprotrophic species ($p < 0.001$, Fig. 4).

Biotic and abiotic influences on spatial fruiting characteristics

The effects of temperature and precipitation on the spatial fruiting characteristics (range, field variance and zero probability), and interactions between fruiting characteristics, were investigated through a regression analysis (Fig. 5, Supplementary material Appendix 1, Table A5) in which a treatment contrast was used for the functional group. This implies that the difference between ECM and saprotrophic species is represented by the term *sapro* (Fig. 5).

A) Relationships of presences and absences

The range (patch size) and field variance estimated from presence-absence data were highly correlated (Fig. 5a). The field variance increased with a wider range and higher zero-probability (Fig. 5a; blue lines), but the relationship of range to the field variance was influenced by climate as well as functional groups (Fig. 5a; red lines). Wider patches (increasing range) were associated with a higher field variance, notably for the ECM species, as indicated by the negative interaction of field variance and functional group (Fig. 5a, red lines). This suggests a stronger separation of presences and absences for ECM than for saprotrophic fungi.

Temperature affected the relationship between the field variance and the range, independent of functional group. At

Figure 2. The posterior distribution of the parameters for the full spatiotemporal characteristics for the presence–absence data (a, b, c) and the fruit body count data (d, e, f, g), i.e. the zero-inflation model. Each model provides estimates for the range (patch size; (a) and (d)), the field variance (amplitude; (b) and (e)), and the autoregressive AR1 parameter (continuity; (c) and (f)). In addition, the models for count data include a zero-probability estimate (g) which is equivalent to $1 - \text{prevalence}$. The posterior distributions for the ECM and saprotrophic species are shown as red and blue lines, respectively. The three plots 47, 54 and 59 are indicated by circles, triangles and squares, respectively. Each of the posterior distributions was scaled to unit maximum.

the same time, increasing temperature reduced the difference in range between the functional groups (Fig. 5a, red lines). In contrast, precipitation did not influence their range or

field variance directly (Fig. 5a), but the annual number of fruit bodies, i.e., the yield, increased with increasing precipitation (Fig. 5b, blue lines).

Figure 3. The expectations from the posterior distributions of the spatial characteristics; range (a, c) and field variance (b, d), for the logistic model of presence-absence (a, b) and fruit body counts (c, d). The marginal posterior distribution is estimated separately for each year, nutritional mode (ECM and Saprotypic species, red and blue, respectively), and plot (plots 47, 54, and 59 indicated by circles, triangles and squares, respectively). The lines are loess smoothers with span = 1, with approximate confidence intervals. The full posterior distribution of each combination of year, nutritional mode and plot is provided in Supplementary material Appendix 1, Fig. A2 and A3. A logarithmic scale (base = 2) is used both for range and field variance.

Unexpectedly, the size of the patches (range) was independent of the number of fruit bodies produced (the

Figure 4. Timelines for zero probability (1 – prevalence) for each of the three plots 47, 54 and 59, drawn as circles, triangles and squares, respectively. The ECM species and saprotrophic species are represented by red and blue lines, respectively. The zero probabilities are the expected tendency calculated from the marginal probability distribution gained from models estimated separately for each combination of year, nutritional mode and plot. The lines are loess smoothers with span = 1, with approximate confidence intervals. The full posterior distribution of each combination of year, nutritional mode and plot is provided in Supplementary material Appendix 1, Fig. A4.

yield; Fig. 5a) while at the same time the yield influenced the field variance (Fig. 5a, blue lines), for which contrasting patterns were found for the functional groups (Fig. 5, blue lines, sapro indicates difference between ECM and saprotrophic species). For ECM species a high yield corresponded to a high field variance, which suggests a more pronounced differentiation between patches with low and high probability of occurrences. In contrast, for saprotrophic species a high yield corresponded to low field variance, again independent of the range (Fig. 5a, blue lines). Note that the variance in annual yield of saprotrophic species was just 22% of the variance for ECM species; hence the variation in field variance related to variation in yield was less noticeable for saprotrophic than for ECM species.

B) Prevalence and yield

The prevalence (1 – P_{zero}) increased with increasing precipitation and decreasing temperature (Fig. 5b). This indicates a climatic influence on occupancy, i.e. the number of sub-subplots occupied. As expected, the yield and the zero-probability were negatively related to each other. The latter relationship decreased in strength as the temperature increased (Fig. 5b, red lines). Furthermore, precipitation was the only climatic variable that influenced the yield (Fig. 5b blue lines), indicating that the influence of precipitation on zero-probability was both direct and indirect (through yield). Both yield and prevalence differed strongly between functional groups (Fig. 5b).

Figure 5. Flow diagrams summarizing the models related to: (a) the spatial characteristics (GMRF) of the logistic model of presence-absence data, (b) the yield and zero-probability parameter of the zero-inflated Poisson model, and (c) the spatial characteristics (GMRF) of the zero-inflated Poisson model of fruit body count data. The numbers in the flow diagrams are the estimated coefficients from the models. (a) The red lines represent the backward elimination model (lme) of the annual expected ranges (posterior distributions; Supplementary material Appendix 1, Fig. A2), the blue lines represent the backward elimination model (lme) of the annual expected field variance (posterior distributions; Supplementary material Appendix 1, Fig. A2). (b) The red lines represent the backward elimination of effects on the expected zero probability (Pzero, red lines), and the blue lines show a model for the sensitivity of the annual fruit body production (yield). (c) The red lines represent the backward elimination model (lme) of the annual expected ranges (posterior distributions; Supplementary material Appendix 1, Fig. A3), the blue lines represent the backward elimination model (lme) of the annual expected field variance (posterior distributions;

C) Fruit body count relationships

No relationship between range and field variance of fruit body counts was found (Fig. 5c), in contrast to the strong relationship noted for presence-absence observations. As expected, the annual range was smaller for saprotrophic than for ECM species (Fig. 5c; red lines). The spatial range for fruit body counts increased when the prevalence decreased, i.e., when the zero-probability increased (Fig. 6). This indicates that the number of fruit bodies produced in years with few sub-subplots occupied were on average more evenly distributed. However, high zero probabilities were associated both with small and large ranges (Fig. 6).

The climatic variables did not influence the range and had a minor effect on the field variance (Fig. 5c) which was mainly influenced by the combination of yield and prevalence (Fig. 5c; blue lines), i.e. the density of fruit bodies. With increasing yield and decreasing prevalence the amplitude (field variance) of fruit body production increased.

Discussion

Our analyses of 15 yr of fruit body census data revealed clear differences in the spatial and temporal organization of ECM and saprotrophic species. The main difference was that fruit bodies of ECM species occurred in larger and more distinct patches, whereas saprotrophic species occurred in smaller patches with variable fruit body production. Interestingly, the nature of these differences depended on whether we considered presence-absence or the abundance of fruit bodies as the response variable. These two responses highlight complementary aspects of fungal fruiting patterns, and combined shed light on basic fungal ecology.

Spatiotemporal characteristics

The statistical models allowed us to quantify the patchiness of fungal fruiting in a unique manner compared to previous studies. The estimated continuity (AR1) described the inter-annual reappearance of fruiting, whereas the estimated amplitude (field variance) of fruit bodies was used to assess the size (range) and distinctness of patches, which intuitively represents a way to quantify 'hot' and 'cold' patches with respect to fruiting. In general, we found a high level of

Figure 5. (Continued)

Supplementary material Appendix 1, Fig. A3). Continuous thick lines represent highly significant paths ($p < 0.001$), continuous thin lines represent significant paths ($p < 0.05$), and dotted lines represent insignificant main effects associated with significant interactions. Lack of lines connecting two boxes indicates that there is no significant relation to the response in question. The specific responses are indicated by boxes casting a shadow. The squares are parameters estimated by the Bayesian models, including range, field variance and zero probability (Pzero). The ellipses represent biological variables, i.e., nutritional mode (Sapro = Saprotrophic – ECM) and yield, and diamond-shaped boxes represent climate covariates, i.e. annual precipitation and annual mean temperature. A treatment contrast is used for nutritional mode, hence the nutrition effects represent the difference introduced by saprotrophic species, hence the box label Sapro.

Figure 6. The relationship between ranges (in m) estimated from the fruit body count data and the zero-probability ($1 - \text{prevalence}$) for ECM and saprotrophic species, red dots and lines and blue dots and lines, respectively. The data include the expected range and zero probabilities for all combinations of plots and years.

continuity of fruiting patterns on the forest floor both for ECM and saprotrophic species, showing that the patterns of 'hot spots' and 'cold spots' for fungal fruiting are persistent over years (Fig. 2). The hot spot continuity indicates inter-annual successful fruiting, but the cold spots may include repeated unsuccessful fruiting or absence of mycelia due to insufficiency of available resource, or inhibited by fungal species not or rarely producing fruit bodies at the particular sub-subplot. The high continuity of fruit body production by saprotrophic fungi was surprising, with a consistency of fruit body counts that was even marginally higher than for ECM species. This is understood as either 1) substrates suitable for saprotrophic fungi were maintained in the same places over periods of years, and/or 2) these fungi have evolved a life-history strategy characterised by frequent fruiting in patches once the necessary amount of resources has been acquired. Firstly, consistent patterns of resource input may result from the consistent leaf fall patterns based on the geometry of trees, from the longevity of dead-wood substrates, and also from topographic features that affect the local distribution of substrates and/or water. Secondly, the potentially transient nature of the resources utilized by saprotrophs may favour a life-history with regular fruiting because this favours dispersal to, and colonisation of, both adjacent and nearby resource patches in the area. The varying size of individual resource patches before other saprotrophic species, may also underlie the evolved tendencies for some saprotrophs to produce clusters of fruit bodies (Moore et al. 2008). Following this strategy, the fruit body production of saprotrophic species would be expected to be relatively unaffected by resource depletion and less influenced by inter-annual climatic variability than that of ECM fungi. However, in drier Mediterranean environments the fruit body production of the two functional groups responded similarly to increased desiccation stress (Ágreda et al. 2015). Nevertheless, in temperate regions fruit body production may occur when the fruiting potential is reached and terminate when resources becomes unavailable. Such a rapid utilization of resources may be particularly

useful for substrate specialists and early successional species which need to spread and recolonise before they are out-competed by later successional species (Boddy et al. 2007). However, saprotrophic species also include substrate generalists and late-successional species which rely on mycelial growth, hyphal cords, and competitive superiority, and produce fewer fruit bodies (Boddy et al. 2007). Dominance of species with a strategy based on mycelial spread and low investment in fruit body production would result in low amplitude of fruit body counts, i.e. low field variance. In La Chaneaz, the combination of continuity and high amplitude of fruit body counts (Fig. 3d) suggests dominance by species that produce fruit bodies whenever they can, creating spatial heterogeneity in the number of fruit bodies. It is also of interest that the amplitude (field variance) increases over time, which suggests a change towards more erratic fruiting.

In contrast to the saprotrophic species, the high continuity of fruiting among ECM species matched expectations based on the long-term consistency of the location of host-plant root systems. The ECM species are connected to the root system(s) of one or more host plants, and both below-ground activity (Högberg and Read 2006) and fruit body production (Högberg et al. 2001, Büntgen and Egli 2014, Büntgen et al. 2015) is at least partly influenced by the host-climate interactions which provide resources for realization of fruiting potentials (Deacon and Fleming 1992, Smith and Read 2008). The stability of resource supplies from trees allows mycelial growth and potentially also connections with multiple trees in mycelial networks (Simard et al. 1997, Taylor 2006, Beiler et al. 2010). However, although genets may be extensive, they may well be fragmented into separate functional units (i.e. ramets) belowground, each potentially supporting fruit bodies (Dettman and van der Kamp 2001). The availability of resources from trees varies among years, but in a given year the resources may be spatially more evenly allocated, providing an even distribution of fruit bodies, at least at the spatial scale of our study. This combination of stable resource availability and stable resource allocation is supported by the observed high connectivity and relatively low amplitude of fruit body counts for ECM species. A pronounced mycelial growth also accords with the patches of ECM species being both larger and more distinct than observed for the saprotrophic species. The distinctness of the ECM patches is revealed by the higher amplitude for fruit body presence-absence than observed for saprotrophic species, in addition to differences due to patch size and prevalence (Fig. 5a). We found a higher probability of absences (i.e. lower prevalence) for saprotrophic than for ECM species, but during the 15 yr the probability of absence of ECM fungi increased strongly in the 1-m² sub-subplots (Fig. 4). This reduction in prevalence for ECM fungi was associated mainly with reduced yield, which again was influenced by climate (Fig. 5). Plausible explanations for this pattern may be found in the combination of soil climate preventing mycelial development and fruiting, and that the variation in precipitation and temperature during the study may have reduced the availability of resources from host trees, thereby restricting mycelial growth and the fruiting potential. A similar trend of reduced yield coupled with a combination of warmer and drier climate has been observed for truffles in the Mediterranean region (Arnolds 1991,

Beiler et al. 2010, Büntgen et al. 2012, 2015). Interestingly, we do see a similar tendency of reduced prevalence among saprotrophic species, which are not dependent on host tree-climate interactions. This similarity among the functional groups is repeated for annual yield of fruit bodies, which again is corroborated by results from a Mediterranean investigations (Ágreda et al. 2015).

Biotic and abiotic influences on spatial characteristics of fruiting

The most important variables affecting the annual spatial characteristics, i.e. patch size (range) and fruiting amplitude (field variance), were the annual yield and the annual prevalence (1 – zero-probability). Climate, on the other hand, mainly affected the yield and zero-probability (Fig. 5). Direct climate effects on spatial characteristics were limited to temperature influencing the range of presence–absence, whereas a combined effect of temperature and precipitation slightly influenced the field variance of fruit body counts.

Nevertheless, precipitation was positively correlated with yield, i.e. the annual number of fruit bodies produced, and negatively correlated with zero-probability; thus the higher the precipitation the more sub-subplots were occupied by fungal fruit bodies. On the other hand, temperature did not significantly affect the yield, but interacted with yield by reducing the effect of yield on zero-probability. In other words, higher prevalence (low zero-probability) was associated with higher yields, but the magnitude of this effect was reduced at higher temperatures. Similar density-related patterns were also seen in the amplitude of fruit body counts. The field variance, which describes the deviation from average fruiting conditioned on presence, was strongly influenced by an interaction between yield and zero-probability (Fig. 5c). With increasing yield both fruiting amplitude and prevalence increased. Higher fruiting amplitude indicates that when numerous fruit bodies are produced there is a greater difference among occupied sub-subplots. At the same time there are more sub-subplots occupied (low zero-probability) with higher yield. This increased prevalence tends to reduce the field variance of fruit body counts, hence reducing the effect of higher yield on fruiting amplitude. This fruit body density process at sub-subplot level is similar for both functional groups.

In contrast to the strong effect of yield on the amplitude of fruiting, yield had no effect on the spatial extent of fruiting (Fig. 5). In light of the temporal decrease in prevalence, the fruit bodies of ECM species may either 1) spatially contract to some centre of the previous larger fruiting area, or 2) the fruit bodies may appear across the entire fruiting area at varying density, i.e. empty sub-subplots may be dispersed in between occupied cells. The results support the second 2) scenario because yield and range were independent and yield was positively related to field variance for presence–absence data. If the former situation prevailed, we would have expected reduced patch size and possibly reduced association between yield and field variance for presence–absence observations, which was not seen. The second scenario may arise from one large mycelium with a more uneven distribution of fruit bodies, a large mycelium which is fragmented

into smaller functional units, or aggregation of individual mycelia of one or more species.

Although yield and range were unrelated for both groups of fungi, saprotrophic species behaved differently to ECM species in that the saprotrophs showed a decrease in amplitude for presence–absence data with increasing yield. To explain this result, we first note that saprotrophic species had a narrower range than ECM species, as the saprotrophic species were typically more restricted to discrete resource units. Hence, with increasing yield saprotrophic species were found in small patches widely dispersed in the plot which was seen as reduced variation in the probability of occurrence. However, from time to time such occurrences were adjacent and then gave an impression of one, wider, patch. This explains how the range may be independent of the annual yield of saprotrophic species. Hence, the dominating life-history strategy of saprotrophic species manifests itself in independence between range and yield, in combination with reduced amplitude of occupancy across sub-subplots with increasing yield.

A similar relationship between zero-probability and fruit body range was observed for both ECM and saprotrophic species. The possible increase in range with increasing zero-probability may result from sub-subplots with low fruiting potential being more likely lost in periods of low prevalence. If such sub-subplots occur in between sub-subplots of higher fruit body counts there will be a change from a considerable difference across a short distance, i.e. short range, towards a potentially less variable situation across a broader range. This, as the count part of the zero-inflated model, is conditioned on a least one presence, and the absences contribute through a logistic section of the zero-inflated likelihood-function. However, with low prevalence both wide and narrow ranges appear dependent on the variability of fruit body production among occupied sub-subplots. Higher prevalence gives dispersed hotspots of intense fruiting with a marked difference across shorter distances. Such processes may account for the observed triangular relationship between range and zero-probability (Fig. 6), with short ranges of fruit body counts being associated with high prevalence and both short and wide ranges potentially associated with low prevalence.

Conclusion

Climate variables such as temperature and precipitation are known to be major determinants of broad-scale patterns such as species distributions and richness gradients, and distributional shifts (Woodward 1987, Pearson and Dawson 2003, Araújo et al. 2005, Thuiller et al. 2005, Menéndez et al. 2006, Grytnes et al. 2014). However, because broad-scale patterns change as the result of demographic changes at the scale of individuals, climate has to impact local and regional dynamic processes to bring about broad-scale change. Thus, fine-scale processes influence the responsiveness of species to climate-induced shifts, often in complex ways (Araújo et al. 2005, Menéndez et al. 2006, Grytnes et al. 2014), and it is not clear in most cases how ecological processes will respond at fine scales due to buffering of climate effects by local processes (Randin et al. 2009, Engler et al. 2011, Lenoir et al. 2013). In the present study we show that climate exerts

small direct effects on fine-scaled spatial distributions of fungal fruiting, but that climate nonetheless influences fine-scale spatial patterns indirectly through effects on prevalence (commonness) and productivity (yield) of fungi. Favourable and unfavourable climate is predicted to result in higher and lower yields, respectively, which affect both the prevalence and the variability (field variance) of fruit body production.

The spatial distribution of a mycelium ultimately restricts the distribution of fruit bodies produced by this mycelium. This simple fact explains the observed differences in fruiting patterns between ECM and saprotrophic species. The two functional groups exhibit independence between patch sizes and the overall yield, but for different reasons. Even though saprotrophic species include a wide variety of life-history strategies, the typical strategy manifests itself in smaller patches of fruit bodies that side by side may amalgamate into larger patches. In contrast, the intimate association between ECM species and single or multiple trees gives rise to an uneven distribution of fruit bodies across a broader area, opening up the possibility that smaller patches of fruit bodies are produced even from larger underground mycelia. A future subdivision of the functional groups is possible and may provide additional insight into the spatiotemporal characteristics of fruit body distributions. Nevertheless, the difference between the functional groups is underlined by their contrasting relationships between yield and field variance, and indicates that fruit bodies are important for the local distribution of fungi, although the fruit bodies themselves only constitute a small part of the total fungal biomass.

Acknowledgements – We acknowledge the Research Council of Norway for financial support to the ClimFun project (grant 225043) and all persons responsible for data collection and management. We thank both reviewers for their help improving the manuscript. Requests concerning data availability may be addressed to SE (simon.egli@wsl.ch).

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Supplementary material (Appendix ECOG-02256 at <www.ecography.org/appendix/ecog-02256>). Appendix 1.