Author(s): Norros, Veera; Halme, Panu; Norberg, Anna; Ovaskainen, Otso

Title: Spore production monitoring reveals contrasting seasonal strategies and a trade-off between spore size and number in wood-inhabiting fungi

Year: 2023

Version: Published version

Please cite the original version:

Norros, V., Halme, P., Norberg, A., & Ovaskainen, O. (2023). Spore production monitoring reveals contrasting seasonal strategies and a trade-off between spore size and number in wood-inhabiting fungi. Functional Ecology, 37(3), 551-563. https://doi.org/10.1111/1365-2435.14254

Received: 21 December 2021 | Accepted: 11 December 2022

DOI: 10.1111/1365-2435.14254

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Spore production monitoring reveals contrasting seasonal strategies and a trade-off between spore size and number in wood-inhabiting fungi

Veera Norros[1,2] | Panu Halme[3,4] | Anna Norberg[2,5] | Otso Ovaskainen[3,2,6]

[1]Biodiversity Centre, Finnish Environment Institute, Helsinki, Finland; [2]Organismal and Evolutionary Biology Research Programme, University of Helsinki, Helsinki, Finland; [3]Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland; [4]School of Resource Wisdom, University of Jyväskylä, Jyväskylä, Finland; [5]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland and [6]Department of Biology, Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, Trondheim, Norway

Correspondence
Veera Norros
Email: veera.norros@syke.fi

Funding information
Academy of Finland, Grant/Award Number: 274489 and 309581; Ella ja Georg Ehrnroothin Säätiö; H2020 European Research Council, Grant/Award Number: 856506; Jane ja Aatos Erkon Säätiö; LUOVA Graduate School; Norges Forskningsråd, Grant/Award Number: 223257; Finnish Ministry of the Environment, Grant/Award Number: VN/12351/2021-YM-2

Handling Editor: Katie Field

Abstract

1. Traits related to reproduction and dispersal drive the assembly and dynamics of species communities and can explain and predict how species respond to habitat loss and fragmentation and to the changing climate. For fungi, such links remain poorly known.
2. We examine how spore production rate, a key demographic trait, is influenced by the interaction between environmental conditions and species traits. We monitored the spore production of 97 wood-inhabiting fungal species on 107 decaying logs for 2 years and analysed the data with a hierarchical community model.
3. Our analysis demonstrates clear species differences in seasonal patterns, with spring and summer release dominating in perennial species, contrary to the commonly held view of autumn as the primary "mushroom season". Many species follow a diurnal pattern with a higher spore release rate during the night. Such patterns in release timing have important implications for dispersal, as shown by recent model simulations.
4. The overall level of spore release was negatively correlated with spore size, providing new evidence that fungi face the classic trade-off of investing either in the number or size of offspring.
5. We found that different species within the functional group of wood-inhabiting fungi display alternative strategies in spore release timing and along the trade-off between offspring size and number. Linking our findings to previously reported correlations between spore size and other traits, we propose a new conceptualization of life history strategies in wood-inhabiting fungi, with implications for species' ability to survive the ongoing biodiversity crisis.

KEYWORDS
basidiomycetes, dispersal, fecundity, life history strategy, plant-pathogen interactions, reproductive ecology, wood decay

1 | INTRODUCTION

Spatial processes are central in understanding the structure and dynamics of populations and communities from the landscape to global scale. For sessile organisms, dispersal is coupled with reproduction forming the paramount spatial demographic process (Nathan & Muller-Landau, 2000; Wright et al., 2008). Dispersal and the rate of reproduction determine gene flow and hence the genetic structure of populations and can affect species co-occurrence patterns and interactions (Allbee et al., 2022; Álvarez-Garrido et al., 2019; Bullock et al., 2002). In the ongoing biodiversity crisis (Secretariat of the Convention on Biological Diversity, 2020), traits related to reproduction and dispersal can separate winners from losers through their effect on species' vulnerability to habitat loss and fragmentation (Hanski, 2005; Henle et al., 2004), migration and adaptation capacities in the face of climate change (Clark et al., 2003; Lenoir & Svenning, 2015) and invasive and pathogenic potential (Bebber et al., 2014; Hastings et al., 2005). Indeed, in a recent global analysis of the link between traits and the current risk of extinction in vertebrates and plants, Carmona et al. (2021) showed that large and slowly reproducing species are likely to be among the first to be lost, leading to ecological communities with lower functional diversity.

Dispersal in fungi has traditionally been viewed as passive—beyond the control of individuals—and incredibly pervasive, with millions of spores being transported by wind across great distances, even between continents (Finlay, 2002; Wilkinson et al., 2012). However, recent research has begun to challenge these assumptions. While spores themselves do not generate or control their movement, fungi have evolved many features that affect the probable flight time and distance of their spores, and in that sense allow the control of dispersal over evolutionary time-scales (Nathan et al., 2008). Such features include aerodynamic properties of spores and fruit bodies (Dressaire et al., 2016; Hussein et al., 2013; Norros et al., 2014) and spore discharge mechanisms that can respond to environmental triggers (Pringle et al., 2005; Roper et al., 2010). There is also increasing evidence that despite their theoretically almost unlimited dispersal potential, fungi can be limited by dispersal, as demonstrated for example by isolation effects on the species richness of mycorrhizal fungi (Peay et al., 2010) and the distribution shifts of mycorrhizal fungi lagging behind their host plants (Álvarez-Garrido et al., 2019). Dispersal limitation can occur even where some spores do arrive, for example in the case of rare and specialized wood-inhabiting species that require very specific conditions for establishment and thus a high density of spores to hit the narrow windows of colonization opportunity (Norros et al., 2012). Fungal dispersal has been identified as a research field attracting increasing interest, with wide knowledge gaps (Chaudhary et al., 2022). At the moment, there is no comprehensive understanding of different dispersal strategies in fungi, although interest in the topic is increasing. For instance, Aguilar-Trigueros et al. (2019) studied allometric relationships between spore size and other traits in arbuscular mycorrhizal fungi, and found evidence for the classic trade-off between size and number of offspring that is well documented in many other organismal groups (Einum & Fleming, 2000; Harper et al., 1970; Leishman et al., 2000; Primack, 1987).

One factor that may greatly reduce the scale of successful dispersal in fungi is vulnerability of spores to direct sunlight and other atmospheric conditions (Norros et al., 2015; Rotem et al., 1985). A recent modelling study demonstrated that restricted spore lifetime can drastically affect the pattern of successful dispersal: if vulnerable spores are produced during turbulent conditions (typical during the day in many regions), they stay airborne too long and few ever get back to ground alive (Lagomarsino Oneto et al., 2020). This highlights the role of the timing of propagule release as a key component in a species' dispersal strategy (Reynolds, 2011; Savage et al., 2010, 2012; Schippers & Jongejans, 2005). However, quantitative empirical knowledge of species-specific spore release patterns in fungi is limited.

In this study, we examine the rate and timing of spore production in wood-inhabiting basidiomycete fungi. This polyphyletic group of fungi is characterized by small spores with very low deposition rates (aerodynamic sizes typically in the range of 1–5 μm; Hussein et al., 2013) often produced in large quantities, as evidenced by the familiar sight of a thick layer of spore dust accumulated on or near large perennial fruit bodies of species such as *Ganoderma applanatum* and *Fomes fomentarius*. The high number of small spores has been considered an adaptation to these species' dependency on patchy, ephemeral and unpredictable resources, with the high numbers ensuring that at least some spores land on a suitable site (Kramer, 1982; Parmasto & Parmasto, 1992); however, as for most fungi, there is no direct evidence for such hypotheses of evolutionary constraints and pressures. Many species in this group have been shown to be vulnerable to sunlight (Norros et al., 2015), which combined with their small size leads to the expectation that the time (and site) of spore release can be crucial to avoid transport to higher layers of the atmosphere where they could easily be retained for days or weeks (Lagomarsino Oneto et al., 2020). High dispersal mortality could be one factor behind the finding that several wood-inhabiting species have suffered from habitat fragmentation more than expected based on the loss of habitat area alone (Edman et al., 2004; Hottola & Siitonen, 2008; Nordén et al., 2013; Penttilä et al., 2006). On the other hand, some species seem unaffected or even favoured by habitat fragmentation (Nordén et al., 2013), suggesting that different species exhibit different life history strategies that predispose them for winning or losing under human-induced pressures.

We monitored the spore production of 97 wood-inhabiting fungal species including polypores, corticioids and hydnoids on 107 decaying logs during two growing seasons (May–October) at an old-growth forest site in Central Finland. Using these data, we model the effect of environmental conditions and species traits on the spore production rate per unit fruit body surface. At the species level, we ask to what extent spore production is determined by a seasonal pattern as compared to a diurnal pattern or daily variation in weather conditions, and whether the quality of the woody substrate is reflected in spore production. At the cross-species level, we ask whether spore size and fruit body growth form are related to species' spore production features. We discuss our results in the light of other studies that have discovered correlations and trade-offs related to life history traits in fungi and suggest future avenues for a more complete understanding of fungal life history strategies and their consequences for species' ability to survive the sixth mass extinction.

2 | MATERIALS AND METHODS

2.1 | Study site and fruit body inventory

The research site (Kuusimäki, Muurame; N 62.22°, E 25.48°) is located in the southern boreal vegetation zone (Ahti et al., 1968) in Central Finland. It is a 108 ha large conservation site with a history of slash and burn cultivation in the nineteenth century and abandoned around 1860s. At present, the forest is of high conservation value, mostly due to the occurrence of a high number of threatened wood-inhabiting species. See more detailed description of the study site in Halme and Kotiaho (2012). The study area is owned by the state of Finland, and we obtained a permission to conduct the field work from the government's conservation administrators (Parks & Wildlife Finland, Metsähallitus; permission granted to Panu Halme).

This study was conducted utilizing a setup that was originally initiated to study the phenology of fungal fruiting (Halme & Kotiaho, 2012) and to optimize monitoring methods (Abrego et al., 2016). At the beginning of the study, each of the 107 study logs (29 spruce, 30 pine, 30 birch, 18 aspen) was divided in 4 segments of equal length. The diameter and decay class of each segment was measured once in 2009 and once in 2010. A fruit body inventory was conducted monthly from May to October in 2009 and 2010. In this study, we used the data on polypores and sturdy, long-living corticioid and hydnoid species. We selected these groups because spore production measurements were easier to conduct reliably on their hymenial surfaces than for example on the more delicate agarics. Species identification was generally made in the field and verified microscopically from a fruit body sample where necessary. Species identification followed mostly Niemelä (2005) and Hjortstam et al. (1988), and the nomenclature follows the Finnish Biodiversity Information Facility database (von Bonsdorff et al., 2022). The list of sampled species is given in Table S1 in Supporting Information.

2.2 | Spore production measurements

Spore production was measured by collecting spore prints on plastic foil pieces that were attached by pins closely to the hymenium (Figure 1a). Spores were allowed to settle on the foil pieces (3, 10 or 40 cm^2) for 14–48 h, always spanning over at least one whole night. Foil size was chosen according to the size of the sampled fruit body, aiming to obtain as large a sample as possible with no part of the foil left outside the hymenium, with the foil piece still fitting into a 1.5 ml or 5 ml sampling tube. We aimed at a spore collection time of 24 h; however, the realized sampling times varied for logistic reasons, as the sampling was fitted into a field campaign whose primary aim was the repeated inventory of all basidiomycete fungi occurring on the 107 study trunks (Halme & Kotiaho, 2012). After collection, each foil piece was suspended in 1 ml of 70% ethanol in a microtube to detach the spores, and the concentration of spores in the resulting suspension was determined. Taking into account the volume of the suspension, the collection time and the surface area of the foil pieces, we calculated the average spore production per square centimetre of hymenium and per hour.

We note that the plastic foil is likely to make the microenvironment of the covered hymenium more humid, which may artificially increase the rate of spore release in our data. However, for our study questions, we considered the risk of such a uniform bias a better option than the alternative of leaving a clear gap between the hymenium and the foil, which would lead to spores escaping at varying rates depending on spore size and weather conditions.

Spore prints were taken at each inventory in 2009 and 2010. For each log segment, one spore print was taken from all study species fruiting on the segment; thus, each species was represented by 1–4 samples per occupied log per visit. For each segment and species, the foil piece was placed on a part of the hymenium that appeared to be the most viable. Clearly dead fruit bodies were not sampled. The spores were counted microscopically in a haematocytometer in 2009 and for May–June in 2010. For the rest of the 2010 samples, we gained access to a particle counter that quantifies particles suspended in an electrolyte (Beckman Coulter Counter model Z2, Beckman Coulter, Inc.), speeding up the counting process. As a control, some of the Coulter counted samples were also counted microscopically to ensure the consistency of the data. The Coulter and microscopic counts were consistent for samples with a moderate-high spore concentration (a clearly distinguishable peak in the particle size distribution) but not for low-concentration samples. Thus, low-concentration Coulter samples were reanalyzed microscopically and, where different, the microscopic count was adopted as the more reliable value.

For 2009 and 2010, weather data was obtained from the Jyväskylä airport weather station of the Finnish Meteorological Institute (62.40°N, 25.67°E), 23 km from the study site. In 2010, six data loggers (HOBO U12-012, Onset Computer Corporation) were also used to measure temperature, relative humidity, and light intensity directly at the study site at 10 min intervals from May to October. We also measured the precipitation at the site with a rain

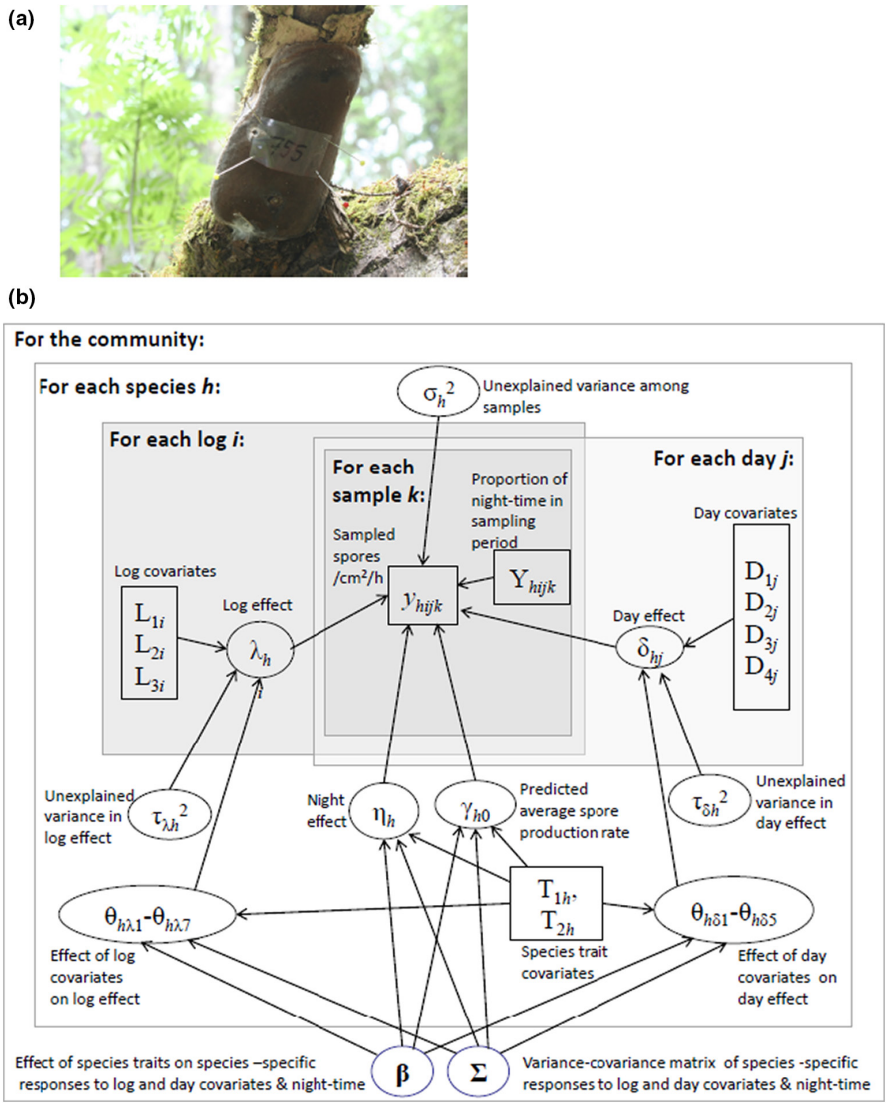

FIGURE 1 (a) Spore production was measured by allowing spores to settle on a piece of plastic foil pinned to the hymenium of the fruit body (here *Phellinus tremulae*). Photograph by Panu Halme. (b) Directed acyclic graph (DAG) presenting the structure of the hierarchical model used to analyse the effect of environmental factors and species traits on spore production rate. Measured variables are shown as rectangles, model parameters as ellipsoids. The grey frames indicate different hierarchical levels.

gauge that was checked and emptied at approximately weekly intervals from May to October 2010. Weather data for the sampling days is shown in Figure S1 in Supporting Information.

For consistency, we adopted the weather data collected at Jyväskylä airport in the modelling described in the next section. The relative humidity values measured at the study site in 2010 were generally higher than those at the urban environment of the airport. However, the pattern of day-to-day variation was similar at both sites; thus, we interpret the relative humidity covariate (D_4) as describing how humid the day was compared to other days, not as a precise description of the microclimate experienced by the fungi.

2.3 | Modelling the effect of environmental factors and species traits on spore production

When considering the population dynamics of wood-inhabiting fungi, the smallest unit of interest is typically one substrate unit (decaying log, standing tree or other type of wood), as it is not possible to assign fruit bodies growing on the same substrate unit to different individuals without genetic analyses. At any given time, the total rate of spore production (spores h^{-1}) by the fruit bodies of a given species growing on one substrate unit (here a decaying log) is the product of the average spore production rate per unit area of the spore-producing fruit body surface called hymenium (henceforth called hymenial spore production rate; spores cm^{-2} h^{-1}) and the area of the hymenium (cm^2) on the log. The hymenial spore production rate and the hymenial area change at different time-scales and can be affected by environmental effects in different ways. Our analysis focused on the hymenial spore production rate, which has received very little attention compared to the more abundant existing data on fruit body abundance.

We adopted a hierarchical community modelling approach (Ovaskainen & Soininen, 2011; Royle & Dorazio, 2006) related to the more comprehensive Hierarchical Model of Species Communities (HMSC; Ovaskainen et al., 2017; Tikhonov et al., 2020), to quantify the effect of the time of year, environmental factors and species traits on hymenial spore production rate (Figure 1b). In this approach, we model each response variable at the level of individual species, and then combine the species-specific models into a single

FIGURE 2 Community level results of the hierarchical community model. The figure illustrates the average level (intercept) of and the effect of species traits (rows) on the environmental responses (columns) of spore production rate. Red or blue colours respectively indicate positive or negative effects of each trait on each environmental response, and the three levels of colour intensity correspond to three different levels of posterior probability: >95%, 90%–95% or 80%–90%. Corresponding species-level results are given in Figure S2 in Supporting Information.

community level model. Thus, we analyse the effect of environmental covariates on each species as well as the influence of species traits on such responses in a single model fitting. Below, we briefly describe the main components and covariates included in the model; for a more detailed description including equations see Appendix S1 in Supporting Information. The model was implemented in Wolfram Mathematica 11 (Wolfram Research, Inc.).

Hymenial spore production rate was modelled on the condition of presence, that is a zero value means that spore production was measured from a live fruit body but the rate was below the detection threshold imposed by our counting method. By contrast, logs with no live fruit bodies were not included as observations of spore production for the species in question. To allow the inclusion of the zero values, we added one counted spore to all microscopy counts and the smallest nonzero value given by the Coulter counter to all raw Coulter counts (140 spores ml^{-1}) prior to the log-transformation.

We assumed that for each species the environmental determinants of spore production of species *h* at a given time can be divided into two additive effects: the effect of the log *i* on which the fruit bodies are growing (λ_{hi}) and the effect of the measuring day *j* (δ_{hj}) (Figure 1b). Furthermore, we allowed hymenial spore production rate to vary between day and night by including the explanatory variable Y_{hijk}, the proportion of night-time (time between sunset and sunrise) in the spore collection period. At the log level, we included three covariates: tree species (L_1; categorical variable), log-transformed basal diameter (L_2) and decay class (L_3), the last two as measured in the first study year 2009. Decay stage was measured as an ordered categorical variable with values 1–5, but for simplicity, we modelled it as if it were continuous, including also a second order term to allow for a maximal spore production at an intermediate decay stage.

The time of year can influence biological processes directly, as in seasonal biorhythms induced by changes in day length, or indirectly through seasonal patterns in weather conditions such as temperature and precipitation. However, many weather variables, such as daily mean temperature, are tightly correlated with the time of year. The effect of the time of year and these weather variables are very difficult to separate in our data, which covers only 2 years. Thus, in addition to the year (D_1; 0 for the first year, 1 for the second year) and the time of year (D_2, defined as the calendar day), we included only two weather-related day-level covariates: the sum of the precipitation in the 24 h preceding the start of the measurements (D_3) and the residual mean relative humidity of the measuring day, after accounting for the correlation of relative humidity with calendar day (D4). We included a square term of calendar day in the model to allow a unimodal seasonal pattern.

At the community level, we modelled the effect of species traits on the species-specific responses to the environmental covariates defined above (Figure 1b). We included two species traits as covariates in our model, with trait data derived from taxonomic literature (Hjortstam et al., 1988; Niemelä, 2005): spore size (T_1; measured as the log-transformed spore volume) and fruit body growth form (T_2; two categories: pileate or resupinate).

We estimated the model parameters using a Bayesian MCMC approach (Gelman et al., 2004). Before model fitting, we standardized all covariates to zero mean and unit variance. We used uninformative conjugate priors that allowed the posterior distributions to be Gibbs sampled directly from the conditional posterior distributions. The priors and sampling distributions for the estimated parameters are given in Appendix S1.

We note that our model assumes that similarity in the spore release patterns of different species can arise through similar traits but is independent of the species' phylogenetic relatedness. To control for the effect of shared phylogeny on the results a posteriori, we performed Pagel's version of phylogenetic generalized least squares (PGLS) regression (Pagel, 1999; as recommended by Revell, 2010) of the estimated level of spore release against the relevant traits. This analysis is related to an OLS regression with phylogenetically independent contrasts but additionally optimizes the error structure of the residuals based on an estimate of the strength of the phylogenetic signal (the parameter λ; usually between 0 and 1). As the exact phylogenetic relationships of our study species remain unresolved, we used a taxonomy (Index Fungorum, http://www.indexfungorum.org/) with equal branch lengths as a proxy for the phylogeny. The analysis was performed using the packages APE (Paradis et al., 2004)

and PHYTOOLS (Revell, 2012) for the R statistical computing environment (R Development Core Team).

3 | RESULTS

Observed spore production rate varied between the detection threshold ca. 3 spores cm^{-2} h^{-1} and a maximum of ca. 1.5 million spores cm^{-2} h^{-1}. The results of the community model are shown in Figure 2 (community-level results) and Figure S2 in Supporting Information (species-level results). Most of the species had a significant seasonal pattern in spore production (Figure 3, Figures S2 and S3). There were also clear species-specific differences in the seasonal timing of spore production (Figure 3, Figure S3). For the majority of species, peak production occurred in July (36 species, e.g. *Antrodia serialis*) or August (22 species, e.g. *Phellinus ferrugineofuscus*), but several species also demonstrated an earlier seasonal timing (11 species with maximum in May, e.g. *Fomes fomentarius*, 10 species with maximum in June) (Figure S2). Note that as May was the earliest measuring time, the exact timing of the peak production of spring-sporulating species (whether in May or earlier in the spring) could not be determined for these species (Figure 3c,d). Spore production peaked in the autumn months (17 spp. in September, 2 spp. October) only for species with annual fruit bodies that appear late in the season (e.g. most *Postia* species). As seen from the statistically supported (>95% posterior probability) positive effect of spore size on the second order effect of calendar day (Figure 2), species with larger spores generally had a less pronounced unimodal seasonal

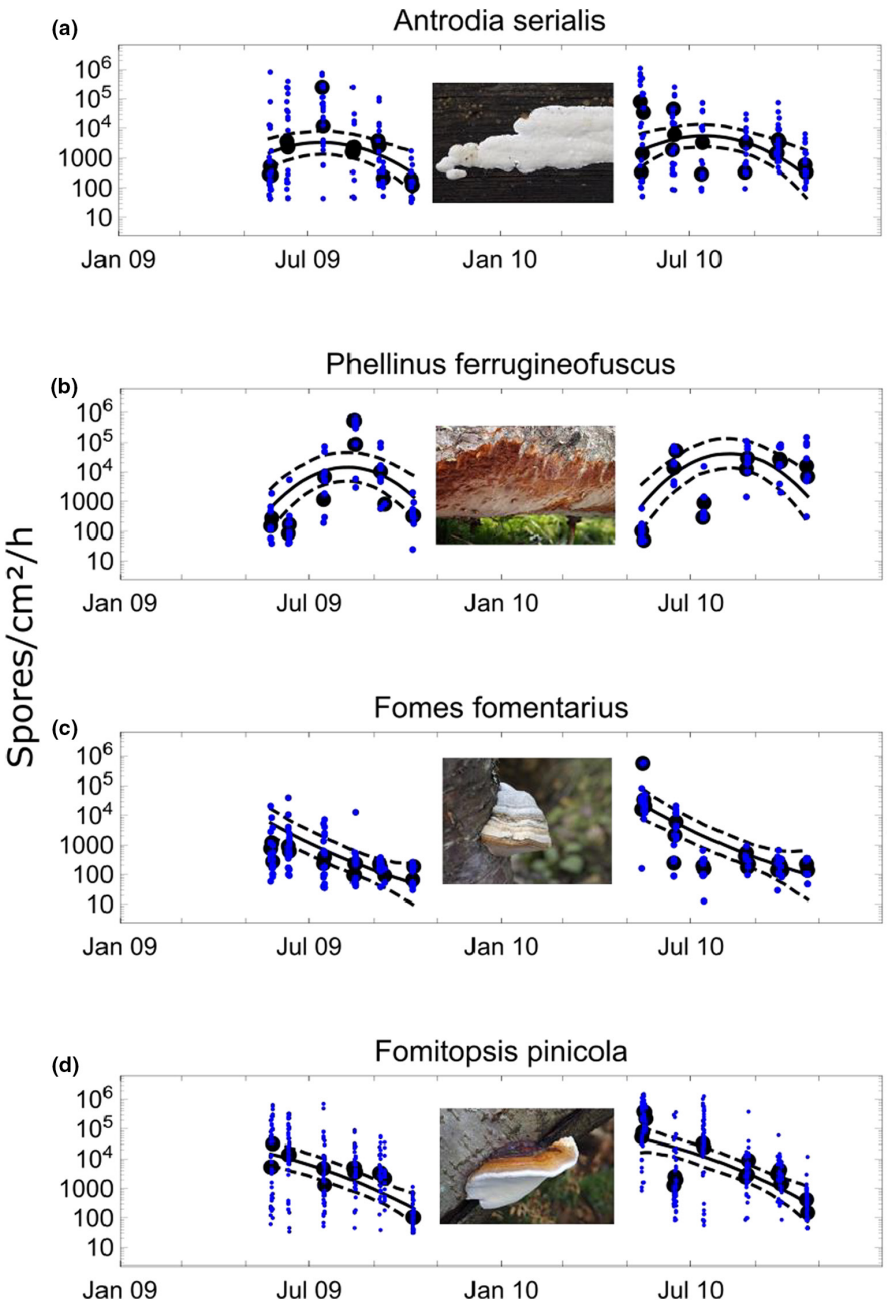

FIGURE 3 The seasonal pattern in spore production rate (spores/cm^2/h) in four example species that showcase the two contrasting seasonal patterns in our data set: summer/autumn producers with a unimodal seasonal pattern (a, b) and spring producers with a decreasing seasonal pattern over the observed period (c, d). The solid and dashed lines show the posterior median and 95% credibility interval of model predictions in which other covariates were set to their average level. The small blue dots show individual observations (i.e. individual plastic foil pieces as shown in Figure 1a) and the large black dots show observed daily means. The seasonal patterns of all species are shown in Figure S3 in Supporting Information. Photographs by Teppo Helo.

pattern. The negative effect of pileate growth form on the first order effect of calendar day (Figure 2) indicates that pileate species tended to have a decreasing seasonal pattern. In other words, species with large spores and pileate fruit bodies generally tended to peak earlier in the season.

Spore production rate was generally higher for samples for which a higher proportion of the collection occurred during the night. We interpret this as a signal of a diurnal pattern in spore release, with higher spore production rate during the night than during the day. The effect of night-time was statistically supported (>95% posterior probability) at the community level (Figure 2) and for 16 of the 97 species at the species level (Figure S2). Spore production also had a generally positive response to residual relative humidity and a negative response to the amount of rain in the preceding 24 h (Figure 2, Figure S2). Nonzero day-level random effects were rare, but there were a few cases of "good days" (and "bad days") on which several species had a higher (or lower) spore production than expected based on the weather conditions included in the model.

Pileate species had a higher level of spore production in our data set, as seen from the negative effect of pileate growth form on the intercept, i.e. the overall level of spore production (Figure 2). Moreover, species-specific spore size was strongly correlated with the species-specific level of spore production: the larger the spores, the fewer spores were produced (Figure 2, Figure 4a). The total volume of produced spores (species-specific spore volume * spore number) was constrained around 100–200 (median value 127) pL spores cm^{-2} h^{-1} (Figure 4b). The most notable exception from this rule was *Ganoderma applanatum*, which was able to produce clearly more, ca. 800 pL spores cm^{-2} h^{-1}. The negative relationship between spore number and size remained highly significant ($p = 0$) in the post-hoc PGLS regression, with a moderate-low phylogenetic signal (Pagel's $\lambda = 0.40$), indicating that spore size and number change together along the phylogeny and their relationship is not an artefact caused by independent phylogenetic structure in spore size and number (Figure S4 in Supporting Information).

Spore production rate was different for fungi inhabiting different tree species (Figure 2, Figure S2). Spore production rate was generally the lowest on pine and the highest on aspen. This seems to be mostly caused by interspecies variation instead of intraspecies variation within those species that inhabit several tree species. By contrast, log diameter and decay class did not have a strong effect on spore production in our data set. There were very few nonzero log-level random effects, that is, spore production was generally not particularly high or low on specific individual logs.

4 | DISCUSSION

Our spore production monitoring revealed several interesting patterns at both community and species levels. The ecologically most relevant results are (1) the confirmation of species-specific differences in the timing of spore release with respect to environmental conditions, time of day and season, (2) the negative correlation between the overall level of spore release and spore size, which indicates a number-size trade-off in wood-inhabiting fungi and has interesting implications for the study of fungal life history strategies. Below, we first discuss each of these main results in a designated subsection. We then outline possible future directions in the study of different life history strategies in fungi, discussing also the relevance of this work for the conservation biology of fungi.

4.1 | The timing of spore release in wood-inhabiting fungi

Environmental conditions, season and the time of day all affected the rate of spore release in our data. It is notable that while the seasonal patterns varied between species, the direction of the effect of environmental factors and diurnal timing was generally consistent across species. For instance, several species released spores predominantly during the night and under humid conditions, while no species showed the opposite response with high statistical support. This suggests that the constraints of shared morphological and physiological features (e.g. the ballistospore discharge mechanism; Fischer et al., 2010; Pringle et al., 2005) determine the general environmental responses but different timing emerges either from subtle variations in the responses or by internal biorhythms achieved through unknown mechanisms. Manipulative experiments are ultimately needed to reveal the critical mechanistic triggers behind the patterns.

One example of an environmental response that would merit a closer mechanistic look in future work is the negative effect of rain on spore production rate, which was contrary to our expectations and appears to be in inconsistent with the positive effect of relative humidity. One possible explanation is that spores are released most effectively when humidity first rises beyond some critical level after a drier period, after which the release rate starts to drop as the spore reserves become exhausted and the internal production rate starts to limit the process. In this case, rain in the preceding 24 h would indicate that the peak release rate was in fact reached before the start of the sampling. Another possibility is that rain during the sampling itself (correlated with rain in the preceding 24 h) led to some spores being lost from the plastic foil pieces.

Theoretical studies describe a trade-off between earlier reproduction, resulting in less vegetative growth, and later reproduction, when more vegetative growth has taken place, allowing for a higher rate of reproduction (Cohen, 1971, 1976). Also, the length of co-occurring vegetative and reproductive growth is expected to vary between species, which is potentially related to variability in the length of the growing season. Many wood-inhabiting fungi have robust perennial fruit bodies that can live for several years and would seem to give the species the potential to sporulate at any time of the year, since the requirement for extensive vegetative growth per growing season is relaxed. Interestingly, in our data all such species had their spore production peak either in the spring, midsummer or late summer—and not in the autumn when the diversity and abundance

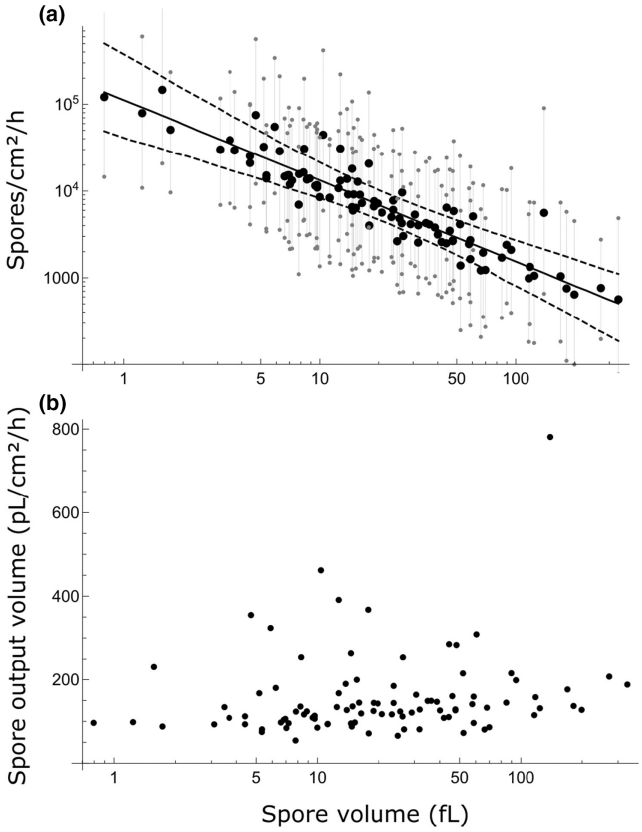

FIGURE 4 (a) Trade-off between spore size and number. The solid line shows the median predicted response of spore production level to spore size, while the black dots show the average spore production level estimated for each species, with other covariates at their average levels. The dashed lines and error bars show the 95% credibility intervals of the predictions. (b) Species-specific spore output volume obtained by multiplying species-specific spore volume by the median predicted spore production level under average conditions. The outlier species with high spore output (ca. 800 pL cm^{-2} h^{-1}) is *Ganoderma applanatum*.

of annual species are the highest (Halme & Kotiaho, 2012). One can hypothesize that for many species the conditions for either dispersal or establishment are in fact as good or better earlier in the season than in the popularly known "prime mushroom time". This is consistent with an earlier study based on aerial samples, indicating that fungal and especially ascomycete diversity in the air is highest in early summer months (Abrego et al., 2018). Ongoing global efforts to map the airborne diversity of fungi (Abrego et al., 2020; Ovaskainen et al., 2020) will bring a wealth of new information on such seasonal patterns and their variation between regions and fungal groups.

Airborne spore monitoring or field sampling covering the whole year would also be required to confirm the exact timing of the peak production, particularly for the spring-sporulating species. While the snow cover at our study site typically persists until May, it is possible that perennial fruit bodies free of snow (particularly on standing trees) start sporulating considerably earlier. In the semiquantitative whole-year monitoring of polypore spore production performed by Nuss (1975) in temperate Central Europe, several perennial species remained active throughout the year, whenever the temperature was above the freezing point.

It is well established that the timing of propagule release can have a major effect on the airborne dispersal pattern, particularly on the probability of long-distance dispersal (Jongejans & Telenius, 2001; Savage et al., 2010; Schippers & Jongejans, 2005; Soons et al., 2004). For fungal spores, an empirical demonstration of this effect is difficult to achieve due to the poor detectability of spores and the large spatial scale of their dispersal caused by their small size (Wilkinson et al., 2012). However, recent work based on atmospheric model simulations has highlighted the effect of both diurnal (Lagomarsino Oneto et al., 2020) and seasonal timing (Wang et al., 2021) on fungal dispersal. Lagomarsino Oneto et al. (2020) showed that diurnal timing can be critical for species whose spores are vulnerable to atmospheric conditions such as sunlight, including many wood-inhabiting fungi (Norros et al., 2015). According to the simulations of Lagomarsino Oneto et al. (2020), vulnerable spores should be released during the night to maximize survival, and the diurnal patterns in our data are consistent with this result. Similar modelling approaches could be adopted to assess how fungal dispersal is affected by the seasonal variation in atmospheric conditions (including irradiance and the probability of rain) and canopy conditions (more deposition surface provided by deciduous trees during the summer) in our study region. This would bring new mechanistic insight into the reasons behind the seasonal patterns we discovered.

4.2 | Trade-off between the size and number of offspring and its implications for life history strategies in wood-inhabiting fungi

We found that species with larger spores produce them in smaller numbers. This general trade-off between the size and the number of offspring has been shown in animals and plants (Dalling & Hubbell, 2002; Einum & Fleming, 2000) but, to our knowledge, only once before in the fungal kingdom (arbuscular mycorrhizal fungi; Aguilar-Trigueros et al., 2019). The relatively constant total volume of produced spores suggests that there are fundamental physiological constraints limiting spore output. The most notable outlier from the constant, *Ganoderma applanatum*, belongs to a genus that is widely known to produce a very high number of spores (Grinn-Gofroń & Strzelczak, 2011), but there are no studies explaining this phenomenon. *Ganoderma* species are characterized by thick-walled, pigmented spores which do not superficially appear less costly to produce than spores of other taxa. Possibly *Ganoderma* are especially efficient in transforming the derived resources to spore production, but the specific underlying physiological features remain to be discovered.

The trade-off between spore size and number provides a new key piece in the puzzle of how the traits of fungi are combined into different strategies that are adaptive under different conditions. As illustrated in Figure 5, spore size is a central trait that has been previously shown to be correlated with several other traits across

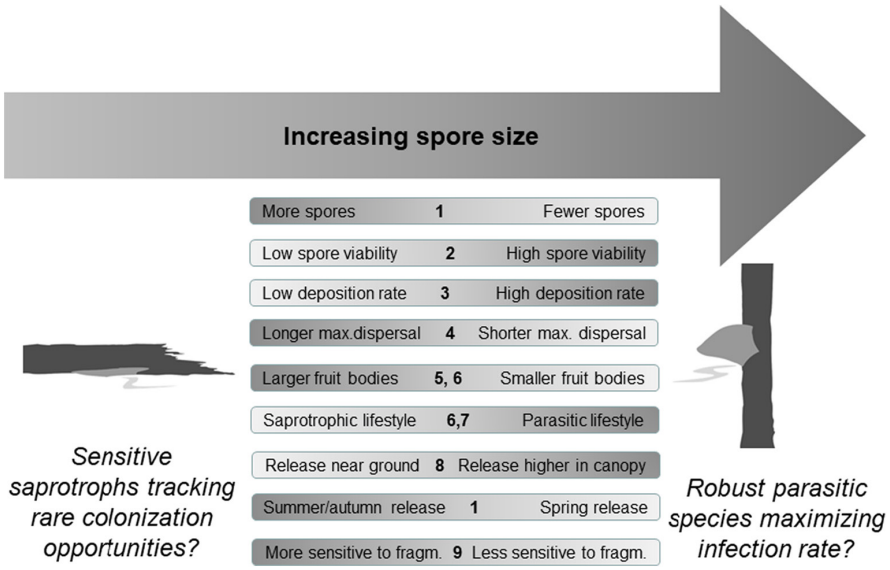

FIGURE 5 Summary of the reported correlations between spore size and other traits in wood-inhabiting fungi. A hypothesis of two contrasting life history strategies is emerging from the patterns (see Box 1). References: (1). The present study, (2) Norros et al. (2015), (3) Hussein et al. (2013), (4) Norros et al. (2014), (5) Meerts (1999) (note: considers all Agarics, not specifically wood-inhabiting fungi), (6) Kauserud et al. (2008), (7) Parmasto and Parmasto (1992), (8) Norros and Halme (2017) (note: stronger correlation reported between spore release height and parasitic/saprotrophic lifestyle than with spore size) and (9) Nordén et al. (2013); "fragm." refers to habitat fragmentation.

wood-inhabiting and other basidiomycete species. Species with large spores tend to have more viable spores (Norros et al., 2015), they have high deposition rate (Hussein et al., 2013) and thus shorter probable residence time and dispersal distance (Norros et al., 2014), larger fruit body size (Kauserud et al., 2008; Meerts, 1999) and their nutritional mode is more often parasitic (Kauserud et al., 2008; Parmasto & Parmasto, 1992). Moreover, spore size has been related to the species-specific response to large-scale habitat fragmentation: species vulnerable to fragmentation tend to have smaller spores (Nordén et al., 2013). We propose that these correlations stem from the existence of different life history trait syndromes or strategies. Specifically, we hypothesize that life history strategies of wood-inhabiting fungi fall along the axis from saprotrophic species that colonize dead wood to parasitic species infecting live trees (Box 1). According to this hypothesis, specialized saprotroph strategy in a continuous forest landscape favours many small spores for tracking the ephemeral resource. Conversely, a parasitic strategy with more colonization opportunities but a higher need for resources to overcome host defences would favour large spores. This interpretation of the reported trait correlations is obviously speculative and oversimplified, but it can provide a starting point for a more refined characterization of life history strategies and their empirical confirmation.

4.3 | Future directions in the study of life history strategies of wood-inhabiting fungi

The establishment stage in the life cycle of wood-inhabiting fungi remains particularly poorly understood (Halbwachs et al., 2015). How and at what stage (live/recently dead/decayed) do different species enter the wood, and what is the germination and colonization probability of an individual landing spore? The starting point for any testing of our hypothesis is the placement of species along the parasitic-saprotrophic axis (Figure 5). It is straightforward to identify species fruiting on living trees as parasitic (although even these may in fact decay dead parts of living trees) but other species could infect live trees while delaying fruiting until the tree has died. Molecular methods such as eDNA metabarcoding from wood samples provide new tools for a more comprehensive understanding of fungal colonization and succession in wood (Ovaskainen et al., 2013). Manipulative experiments introducing and following the colonization of new substrate under controlled conditions while monitoring fungal species composition in the air (Abrego et al., 2018; Ovaskainen et al., 2020) would be particularly useful for uncovering the factors determining the first steps of colonization.

Airborne eDNA metabarcoding also allows the testing of a few specific hypotheses arising from the proposed idea of contrasting life history strategies. These include at least the following:

- **Vertical gradient in airborne species composition**. If saprotrophic species have evolved adaptations such as low fruiting height and night-time spore release to avoid being transported high in the atmosphere, this predicts a steeper vertical gradient in saprotrophic than parasitic species, with a lower proportion of saprotrophic spores escaping to the free atmosphere above the forest canopy.
- **Patterns of variation in airborne species composition**. If saprotrophic species are successful in avoiding mixing with the free atmosphere, we should see a more homogeneous distribution of

BOX 1 Trait patterns suggest contrasting dispersal optimization between saprotrophic and parasitic life history strategies in wood-inhabiting fungi.

We summarize the reported correlations between spore size and other traits in Figure 5. These patterns suggest that saprotrophic and parasitic wood-inhabiting fungi demonstrate different life history strategies with different priorities for dispersal. We explain this hypothesis by the narrative below.

Saprotrophic species produce a large number of small spores in order to track their ephemeral resource in the surroundings (Parmasto & Parmasto, 1992). Individual spores do not carry much resources and are not long-lived (Norros et al., 2015) but their large number ensures that some arrive on the preferred substrate alive. Their small size helps them spread within the surrounding forest even when they are released very close to the ground in the still night air (Norros & Halme, 2017). These species are vulnerable to habitat fragmentation (Nordén et al., 2013), as their spores cannot survive long in the atmosphere, making the colonization of isolated habitat patches difficult. Moreover, some of the species may require specific conditions for establishment (e.g. wood of a specific type and decay stage or decayed by a certain predecessor species, Nordén et al., 2013), making the windows of colonization opportunity very narrow and difficult to hit by the highly diluted spore rain from a distant source, particularly if the species is rare in the landscape and thus the overall "spore pressure" in the air is low (Norros et al., 2012).

By contrast, the parasitic species have large spores that contain more resources needed to overcome host defences (Kauserud et al., 2008). Their large size and spore release in the canopy (Norros & Halme, 2017) also helps their deposition within the canopy (Hussein et al., 2013; Norros et al., 2014), enabling the spores to infect trees through damaged branches. Spring release makes it likelier for the spores to deposit on branches instead of leaves; moreover, there may be a higher abundance of fresh wounds in the canopy caused by snow in the past winter. Habitat fragmentation is less critical for these species as their spores are more robust and survive longer in the atmosphere and as their colonization opportunities (live trees) are more abundant in the landscape.

parasitic species vs. more local variation in saprotrophic species in the air.

- **Seasonal patterns in airborne species composition**. If parasitic species benefit from springtime spore release, there should be a corresponding seasonal shift in the airborne community composition. Air monitoring could also reveal the more precise starting time of spore release during the early spring, not covered by our on-site monitoring which was limited to the snow-free season.

Finally, understanding how different traits are linked into different dispersal and life history strategies in fungi could enable predicting how different fungal species react to anthropogenic changes, particularly habitat fragmentation and climate change (Chaudhary et al., 2022). Our data provides many starting points for hypotheses, experiments and other work on the topic. One critical question is how different seasonal strategies of spore release are equipped to cope with climate change induced changes in the onset and conditions of different season. For example, spring-sporulating species may start sporulating earlier, which could lead to the exposure of their spores to higher levels of UV radiation in the atmosphere. Spring-producing species could also be faced with increasingly hot, dry summers during their establishment phase. Such question will require increasing attention in future work.

5 | CONCLUSIONS

In this study, we have demonstrated that spore release in different species of fungi follows clearly different biorhythms or responds differently to environmental triggers, even within one group of fungi sharing a common resource. Moreover, we have shown that the total spore output in terms of volume per unit time and fruit body surface area is constrained, but different species divide this volume differently in fewer large or more small spores, consistently with the size-number trade-off described in other groups of organisms. Both spore size and the timing of spore release are predicted to have a strong effect on species' dispersal patterns, suggesting that these traits are evolutionarily fine-tuned to optimize colonization of new resources. Taken together with other reported correlations between traits, evidence is accumulating that life history features of fungi do not vary randomly but correspond to specific strategies, which can be differently predisposed to extinction under anthropogenic pressures. A more mechanistic understanding of fungal dispersal and other life history processes is needed to achieve a better understanding of the different strategies and their consequences.

AUTHOR CONTRIBUTIONS

Veera Norros and Panu Halme had the original idea for the study and designed and carried out the data collection. Veera Norros analysed the data with feedback from Otso Ovaskainen. Veera Norros wrote the manuscript, with significant contributions to the text from Panu Halme, Anna Norberg and Otso Ovaskainen. All authors gave final approval for publication.

ACKNOWLEDGEMENTS

We are indebted to Katja Juutilainen, Henrik Murdoch, Lotta Sundström, Anni Rintoo, Jenna Purhonen, Eeva-Marja Turkki, Noora Vartija and Asta Vaso for their assistance in the empirical work and

Nerea Abrego for helpful discussions that supported the writing of the manuscript. VN was funded by the Academy of Finland (grant No. 274489), LUOVA graduate school, Ella ja Georg Ehrnroothin Säätiö and the Finnish Ministry of the Environment (Finnish Ecosystem Observatory project number VN/12351/2021-YM-2). OO was funded by the Academy of Finland (grant No. 309581), Jane and Aatos Erkko Foundation, Research Council of Norway through its Centres of Excellence Funding Scheme (223257), and the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No 856506; ERC-synergy project LIFEPLAN). We are also grateful to two anonymous reviewers whose constructive comments helped to improve our manuscript.

CONFLICT OF INTEREST

None identified.

DATA AVAILABILITY STATEMENT

The data analysed in this study as well as the model code are available from Zenodo: https://doi.org/10.5281/zenodo.7432805 (Norros et al., 2022).

ORCID

Veera Norros https://orcid.org/0000-0002-7481-0693
Panu Halme https://orcid.org/0000-0002-1751-5858
Anna Norberg https://orcid.org/0000-0002-3520-1043
Otso Ovaskainen https://orcid.org/0000-0001-9750-4421

REFERENCES

Abrego, N., Crosier, B., Somervuo, P., Ivanova, N., Abrahamyan, A., Abdi, A., Hämäläinen, K., Junninen, K., Maunula, M., Purhonen, J., & Ovaskainen, O. (2020). Fungal communities decline with urbanization—More in air than in soil. *The ISME Journal*, *14*, 2806–2815. https://doi.org/10.1038/s41396-020-0732-1

Abrego, N., Halme, P., Purhonen, J., & Ovaskainen, O. (2016). Fruit body based inventories in wood-inhabiting fungi: Should we replicate in space or time? *Fungal Ecology*, *20*, 225–232. https://doi.org/10.1016/j.funeco.2016.01.007

Abrego, N., Norros, V., Halme, P., Somervuo, P., Ali-Kovero, H., & Ovaskainen, O. (2018). Give me a sample of air and I will tell which species are found from your region: Molecular identification of fungi from airborne spore samples. *Molecular Ecology Resources*, *18*, 511–524. https://doi.org/10.1111/1755-0998.12755

Aguilar-Trigueros, C. A., Hempel, S., Powell, J. R., Cornwell, W. K., & Rillig, M. C. (2019). Bridging reproductive and microbial ecology: A case study in arbuscular mycorrhizal fungi. *The ISME Journal*, *13*(4), 873–884. https://doi.org/10.1038/s41396-018-0314-7

Ahti, T., Hämet-Ahti, L., & Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici*, *5*, 169–211.

Allbee, S. A., Rogers, H. S., & Sullivan, L. L. (2022). The effects of dispersal, herbivory, and competition on plant community assembly. *Ecology*, *104*, e3859. https://doi.org/10.1002/ecy.3859

Álvarez-Garrido, L., Viñegla, B., Hortal, S., Powell, J. R., & Carreira, J. A. (2019). Distributional shifts in ectomycorrizhal fungal communities lag behind climate-driven tree upward migration in a conifer forest-high elevation shrubland ecotone. *Soil Biology and Biochemistry*, *137*, 107545. https://doi.org/10.1016/j.soilbio.2019.107545

Bebber, D. P., Holmes, T., & Gurr, S. J. (2014). The global spread of crop pests and pathogens. *Global Ecology and Biogeography*, *23*, 1398–1407. https://doi.org/10.1111/geb.12214

Bullock, J. M., Kenward, R. E., & Hails, R. (2002). *Dispersal Ecology*. Blackwell.

Carmona, C. P., Tamme, R., Partel, M., de Bello, F., Brosse, S., Capdevila, P., Gonzalez—M, R., Gonzalez-Suarez, M., Salguero-Gomez, R., Vasquez-Valderrama, M., & Toussaint, A. (2021). Erosion of global functional diversity across the tree of life. *Science Advances*, *7*(13), 1–12. https://doi.org/10.1126/sciadv.abf2675

Chaudhary, B. L., Aguilar-Trigueros, C. A., Mansour, I., & Rillig, M. C. (2022). Fungal dispersal across spatial scales. *Annual Review of Ecology, Evolution, and Systematics*, *53*(1), 69–85. https://doi.org/10.1146/annurev-ecolsys-012622-021604

Clark, J. S., Lewis, M., McLachlan, J. S., & HilleRisLambers, J. (2003). Estimating population spread: What can we forecast and how well? *Ecology*, *84*, 1979–1988.

Cohen, D. (1971). Maximizing final yield when growth is limited by time or by limiting resources. *Journal of Theoretical Biology*, *33*, 299–307. https://doi.org/10.1016/0022-5193(71)90068-3

Cohen, D. (1976). The optimal timing of reproduction. *The American Naturalist*, *110*, 801–807.

Dalling, J. W., & Hubbell, S. P. (2002). Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *Journal of Ecology*, *90*, 557–568. https://doi.org/10.1046/j.1365-2745.2002.00695.x

Dressaire, E., Yamada, L., Song, B., & Roper, M. (2016). Mushrooms use convectively created airflows to disperse their spores. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 2833–2838. https://doi.org/10.1073/pnas.1509612113

Edman, M., Gustafsson, M., Stenlid, J., Jonsson, B. G., & Ericson, L. (2004). Spore deposition of wood-decaying fungi: Importance of landscape composition. *Ecography*, *27*, 103–111. https://doi.org/10.1111/j.0906-7590.2004.03671.x

Einum, S., & Fleming, I. A. (2000). Highly fecund mothers sacrifice offspring survival to maximize fitness. *Nature*, *405*, 565–567. https://doi.org/10.1038/35014600

Finlay, B. J. (2002). Global dispersal of free-living microbial eukaryote species. *Science*, *296*, 1061–1063. https://doi.org/10.1126/science.1070710

Fischer, M. W. F., Stolze-Rybczynski, J. L., Cui, Y. L., & Money, N. P. (2010). How far and how fast can mushroom spores fly? Physical limits on ballistospore size and discharge distance in the Basidiomycota. *Fungal Biology*, *114*, 669–675. https://doi.org/10.1016/j.funbio.2010.06.002

Gelman, A., Carlin, J. B., Stern, H. S., & Rubin, D. B. (2004). *Bayesian data analysis* (2nd ed.). Chapman & Hall.

Grinn-Gofroń, A., & Strzelczak, A. (2011). The effects of meteorological factors on the occurrence of *Ganoderma* sp. spores in the air. *International Journal of Biometeorology*, *55*(2), 235–241. https://doi.org/10.1007/s00484-010-0329-x

Halbwachs, H., Brandl, R., & Bässler, C. (2015). Spore wall traits of ectomycorrhizal and saprotrophic agarics may mirror their distinct lifestyles. *Fungal Ecology*, *17*, 197–204. https://doi.org/10.1016/j.funeco.2014.10.003

Halme, P., & Kotiaho, J. S. (2012). The importance of timing and number of surveys in fungal biodiversity research. *Biodiversity and Conservation*, *21*, 205–219. https://doi.org/10.1007/s10531-011-0176-z

Hanski, I. (2005). *The shrinking world: Ecological consequences of habitat loss*. International Ecology Institute.

Harper, J. L., Lovell, P. H., & Moore, K. G. (1970). The shapes and sizes of seeds. *Annual Review of Ecology and Systematics*, *1*, 327–356. https://doi.org/10.1146/annurev.es.01.110170.001551

Hastings, A., Cuddington, K., Davies, K. F., Dugaw, C. J., Elmendorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B. A., Moore, K., Taylor, C., & Thomson, D. (2005). The spatial spread of invasions: New developments in theory and evidence. *Ecology Letters*, *8*, 91–101. https://doi.org/10.1111/j.1461-0248.2004.00687.x

Henle, K., Davies, K. F., Kleyer, M., Margules, C., & Settele, J. (2004). Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation*, *13*, 207–251. https://doi.org/10.1023/B:BIOC.0000004319.91643.9e

Hjortstam, K., Larsson, K. H., Ryvarden, L., & Eriksson, J. (1988). *The corticiaceae of north Europe*. Fungiflora.

Hottola, J., & Siitonen, J. (2008). Significance of woodland key habitats for polypore diversity and red-listed species in boreal forests. *Biodiversity and Conservation*, *17*, 2559–2577. https://doi.org/10.1007/s10531-008-9317-4

Hussein, T., Norros, V., Hakala, J., Petäjä, T., Aalto, P. P., Rannik, Ü., Vesala, T., & Ovaskainen, O. (2013). Species traits and inertial deposition of fungal spores. *Journal of Aerosol Science*, *61*, 81–98. https://doi.org/10.1016/j.jaerosci.2013.03.004

Jongejans, E., & Telenius, A. (2001). Field experiments on seed dispersal by wind in ten umbelliferous species (Apiaceae). *Plant Ecology*, *152*, 67–78. https://doi.org/10.1023/A:1011467604469

Kauserud, H., Colman, J. E., & Ryvarden, L. (2008). Relationship between basidiospore size, shape and life history characteristics: A comparison of polypores. *Fungal Ecology*, *1*, 19–23. https://doi.org/10.1016/j.funeco.2007.12.001

Kramer, C. L. (1982). Production, release and dispersal of basidiospores. In J. Frankland, J. N. Hedger, & M. J. Swift (Eds.), *Decomposer basidiomycetes: Their biology and ecology* (pp. 33–49). Cambridge University Press.

Lagomarsino Oneto, D., Golan, J., Mazzino, A., Pringle, A., & Seminara, A. (2020). Timing of fungal spore release dictates survival during atmospheric transport. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(10), 5134–5143. https://doi.org/10.1073/pnas.1913752117

Leishman, M. R., Wright, I. J., Moles, A. T., & Westoby, M. (2000). The evolutionary ecology of seed size. In M. Fenner (Ed.), *Seeds: The ecology of regeneration in plant communities* (pp. 31–57). CABI Pub.

Lenoir, J., & Svenning, J.-C. (2015). Climate-related range shifts – A global multidimensional synthesis and new research directions. *Ecography*, *38*, 15–28. https://doi.org/10.1111/ecog.00967

Meerts, P. (1999). The evolution of spore size in agarics: Do big mushrooms have big spores? *Journal of Evolutionary Biology*, *12*, 161–165. https://doi.org/10.1046/j.1420-9101.1999.00020.x

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 19052–19059. https://doi.org/10.1073/pnas.0800375105

Nathan, R., & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, *15*, 278–285. https://doi.org/10.1016/S0169-5347(00)01874-7

Niemelä, T. (2005). *Käävät, puiden sienet (Polypores, lignicolous fungi)*. Finnish Museum of Natural History.

Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., & Ovaskainen, O. (2013). Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *Journal of Ecology*, *101*, 701–712. https://doi.org/10.1111/1365-2745.12085

Norros, V., & Halme, P. (2017). Growth sites of polypores from quantitative expert evaluation: Late-stage decayers and saprotrophs fruit closer to ground. *Fungal Ecology*, *28*, 53–65. https://doi.org/10.1016/j.funeco.2017.04.004

Norros, V., Halme, P., Norberg, A., & Ovaskainen, O. (2022). vnorros/sporeprod: Supplement to Norros et al. functional ecology (version v1). *Zenodo*. https://doi.org/10.5281/zenodo.7432805

Norros, V., Karhu, E., Nordén, J., Vähätalo, A. V., & Ovaskainen, O. (2015). Spore sensitivity to sunlight and freezing can restrict dispersal in wood-decay fungi. *Ecology and Evolution*, *5*, 3312–3326. https://doi.org/10.1002/ece3.1589

Norros, V., Penttilä, R., Suominen, M., & Ovaskainen, O. (2012). Dispersal may limit the occurrence of specialist wood decay fungi already at small spatial scales. *Oikos*, *121*, 961–974. https://doi.org/10.1111/j.1600-0706.2012.20052.x

Norros, V., Rannik, Ü., Hussein, T., Petäjä, T., Vesala, T., & Ovaskainen, O. (2014). Do small spores disperse further than large spores? *Ecology*, *95*, 1612–1621. https://doi.org/10.1890/13-0877.1

Nuss, I. (1975). *Zur Ökologie der Porlinge. Untersuchungen über die Sporulation einiger Porlinge und die an ihnen gefundenen Käferarten*. J. Cramer.

Ovaskainen, O., Abrego, N., Somervuo, P., Palorinne, I., Hardwick, B., Pitkänen, J.-M., Andrew, N. R., Niklaus, P. A., Schmidt, N. M., Seibold, S., Vogt, J., Zakharov, E. V., Hebert, P. D. N., Roslin, T., & Ivanova, N. V. (2020). Monitoring fungal communities with the global spore sampling project. *Frontiers in Ecology and Evolution*, *7*, 442–447. https://doi.org/10.3389/fevo.2019.00511

Ovaskainen, O., Schigel, D., Ali-Kovero, H., Auvinen, P., Paulin, L., Nordén, B., & Nordén, J. (2013). Combining high-throughput sequencing with fruit body surveys reveals contrasting life-history strategies in fungi. *The ISME Journal*, *7*, 1696–1709. https://doi.org/10.1038/ismej.2013.61

Ovaskainen, O., & Soininen, J. (2011). Making more out of sparse data: Hierarchical modeling of species communities. *Ecology*, *92*, 289–295. https://doi.org/10.1890/10-1251.1

Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, F. G., Duan, L., Dunson, D., Roslin, T., & Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, *20*, 561–576. https://doi.org/10.1111/ele.12757

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, *401*, 877–888. https://doi.org/10.1038/44766

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*, 289–290. https://doi.org/10.1093/bioinformatics/btg412

Parmasto, E., & Parmasto, I. (1992). Size and shape of basidiospores in the Hymenomycetes. *Mycologia Helvetica*, *5*, 47–78.

Peay, K. G., Garbelotto, M., & Bruns, T. D. (2010). Evidence of dispersal limitation in soil microorganisms: Isolation reduces species richness on mycorrhizal tree islands. *Ecology*, *91*, 3631–3640. https://doi.org/10.1890/09-2237.1

Penttilä, R., Lindgren, M., Miettinen, O., Rita, H., & Hanski, I. (2006). Consequences of forest fragmentation for polyporous fungi at two spatial scales. *Oikos*, *114*, 225–240. https://doi.org/10.1111/j.2006.0030-1299.14349.x

Primack, R. B. (1987). Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics*, *18*, 409–430. https://doi.org/10.1146/annurev.es.18.110187.002205

Pringle, A., Patek, S. N., Fischer, M., Stolze, J., & Money, N. P. (2005). The captured launch of a ballistospore. *Mycologia*, *97*, 866–871. https://doi.org/10.3852/mycologia.97.4.866

Revell, L. J. (2010). Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution*, *1*, 319–329. https://doi.org/10.1111/j.2041-210X.2010.00044.x

Revell, L. J. (2012). Phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*, 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Reynolds, A. M. (2011). Exponential and power-law contact distributions represent different atmospheric conditions. *Phytopathology*, *101*, 1465–1470. https://doi.org/10.1094/PHYTO-01-11-0001

Roper, M., Seminara, A., Bandi, M. M., Cobb, A., Dillard, H. R., & Pringle, A. (2010). Dispersal of fungal spores on a cooperatively generated wind. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 17474–17479. https://doi.org/10.1073/pnas.1003577107

Rotem, J., Wooding, B., & Aylor, D. E. (1985). The role of solar radiation, especially ultraviolet, in the mortality of fungal spores. *Phytopathology*, *75*, 510–514.

Royle, J. A., & Dorazio, R. M. (2006). Hierarchical models of animal abundance and occurrence. *Journal of Agricultural Biological and Environmental Statistics*, *11*, 249–263. https://doi.org/10.1198/108571106X129153

Savage, D., Barbetti, M. J., MacLeod, W. J., Salam, M. U., & Renton, M. (2010). Timing of propagule release significantly alters the deposition area of resulting aerial dispersal. *Diversity and Distributions*, *16*, 288–299. https://doi.org/10.1111/j.1472-4642.2009.00634.x

Savage, D., Barbetti, M. J., MacLeod, W. J., Salam, M. U., & Renton, M. (2012). Seasonal and diurnal patterns of spore release can significantly affect the proportion of spores expected to undergo long-distance dispersal. *Microbial Ecology*, *63*, 578–585. https://doi.org/10.1007/s00248-011-9949-x

Schippers, P., & Jongejans, E. (2005). Release thresholds strongly determine the range of seed dispersal by wind. *Ecological Modelling*, *185*, 93–103. https://doi.org/10.1016/j.ecolmodel.2004.11.018

Secretariat of the Convention on Biological Diversity. (2020). *Global biodiversity outlook 5*. United Nations Convention on Biological Diversity (CBD).

Soons, M. B., Heil, G. W., Nathan, R., & Katul, G. G. (2004). Determinants of long-distance seed dispersal by wind in grasslands. *Ecology*, *85*, 3056–3068. https://doi.org/10.1890/03-0522

Tikhonov, G., Opedal, O. H., Abrego, N., Lehikoinen, A., de Jonge, M. M. J., Oksanen, J., & Ovaskainen, O. (2020). Joint species distribution modelling with the r-package Hmsc. *Methods in Ecology and Evolution*, *11*, 442–447. https://doi.org/10.1111/2041-210X.13345

von Bonsdorff, T., Kytövuori, I., Vauras, J., Niskanen, T., Liimatainen, K., Salo, P., Höijer, P., Ohenoja, E., Huhtinen, S., Kosonen, L., Kekki, T., Lahti, M., Kokkonen, K., Toivonen, M., & Ruotsalainen, A. L. (2022). Sienet–Fungi. Checklist 2020. https://urn.fi/URN:ISSN:2490-0907

Wang, M., Kriticos, D. J., Ota, N., Brooks, A., & Paini, D. (2021). A general trait-based modelling framework for revealing patterns of airborne fungal dispersal threats to agriculture and native flora. *New Phytologist*, *232*(3), 1506–1518. https://doi.org/10.1111/nph.17659

Wilkinson, D. M., Koumoutsaris, S., Mitchell, E. A. D., & Bey, I. (2012). Modelling the effect of size on the aerial dispersal of microorganisms. *Journal of Biogeography*, *39*, 89–97. https://doi.org/10.1111/j.1365-2699.2011.02569.x

Wright, S. J., Trakhtenbrot, A., Bohrer, G., Detto, M., Katul, G. G., Horvitz, N., Muller-Landau, H.-C., Jones, F. A., & Nathan, R. (2008). Understanding strategies for seed dispersal by wind under contrasting atmospheric conditions. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 19084–19089. https://doi.org/10.1073/pnas.0802697105

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1.

Figure S2.

Figure S3.

Figure S4.

Appendix S1.

How to cite this article: Norros, V., Halme, P., Norberg, A., & Ovaskainen, O. (2023). Spore production monitoring reveals contrasting seasonal strategies and a trade-off between spore size and number in wood-inhabiting fungi. *Functional Ecology*, *00*, 1–13. https://doi.org/10.1111/1365-2435.14254