



# Mean spore size and shape in ectomycorrhizal and saprotrophic assemblages show strong responses under resource constraints



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## ABSTRACT

Ectomycorrhizal and saprotrophic agaricoid basidiomycetes show diverse morphological reproductive traits, a phenomenon which has been attributed to their different lifestyles. From previous studies, we know that such differences are also reflected in assembly formation. Regardless of these differences, and assuming that dispersal fitness, predominantly by air movement, is one of the prevalent factors in fungal lifecycles, spores of both guilds should become on average more elongate and smaller with resource depletion. In our study we defined resource depletion as the decrease of living and dead organic biomass due to climate constraints along an elevational gradient in the Bavarian Forest (Germany).

We found that spores of both guilds indeed become more elongate along the resource depletion gradient. Unexpectedly, the ectomycorrhizal assemblages showed larger spores under resource constraints, which could be a survivability trade-off. The spore trait syndrome responses to environmental constraints suggest ecological relevance, i.e. being advantageous in environments with patchily distributed resources.

To deepen our mechanistic understanding of the underlying patterns, we particularly recommend experiments (artificial resource gradient free of confounding effects such as climate), and application of genomics and transcriptomics for elucidating the evolution of spore morphology.

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## 1. Introduction

Spores of higher fungi have lost the ability for active dispersal found in the ancestral Chytridiomycota, and at all but the spore stage, their ability to move actively to successfully access new habitats is restricted to mycelial growth (Perrin, 2009). To compensate for the loss of active dispersal, higher fungi, including saprotrophic and ectomycorrhizal agaricoid guilds have evolved a fascinating morphological diversity of dispersal organs, i.e. fruit bodies and spores adapted to passive dispersal (see e.g. Spooner and Roberts, 2005; Knudsen and Vesterholt, 2012). However, our knowledge of the evolution of sexual life history traits in fungi and its ecological relevance is still rudimentary (Pringle et al., 2015). In contrast, a tremendous number of studies have been carried out demonstrating that plant seed traits are adapted to specific

lifestyles (Willson and Traveset, 2000). For example, the European mistletoe (*Viscum album*) has developed spherical and sticky seeds (Reid, 1991), thus adapted to substrate-specific dispersal by birds, whereas the seeds of maples (*Acer* spp.) are winged for optimal wind dispersal. Analogously, in fungi morphological differences of diaspores might also be an adaptation to specific lifestyles. In agaricoid fungi, two main guilds with different trophic modes can be distinguished: saprotrophs decompose organic material to extract carbon, whereas their ectomycorrhizal counterparts receive their carbon from a plant host in exchange for mineral nutrients (Kirk et al., 2011). In contrast to spores of saprotrophic fungi, ectomycorrhizal spores need to reach belowground regions to get close to host roots. Frequently such spores will be forced to stay put for slow-growing roots to pass by (cf. Brundrett, 1991). Only then can germination be triggered by root exudates (Fries et al., 1985; Grayston et al., 1997; Kikuchi et al., 2007). Therefore, ectomycorrhizal spores depend on stored carbon for prolonged survival (Bruns et al., 2009; Nara, 2009; Nguyen et al., 2012). Moreover, as suggested earlier, the stored carbon is needed for growing a germ-tube and mating, which takes place before the fungus receives

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carbon from a distant host (e.g. Halbwachs and Bässler, 2015). In consequence, it should be expected that most ectomycorrhizal agarics produce large spores.

The saprotrophic guild mainly operates the strategy of dispersing and establishing without delay, particularly if they are predominantly a user of ephemeral substrates (Osono, 2003). In most cases, germination and establishment can take place after arriving at a suitable aboveground substrate. Some fungi that colonise fresh litter, may also need prolonged survival if the substrate is only seasonally available. In addition, saprotrophs sometimes require soluble nitrogen to become established, especially on recalcitrant substrates, such as fresh needle litter (Lindahl and Boberg, 2008; Boberg et al., 2011). Overall, saprotrophic fungi do not need pronounced carbon reserves in their spores, and can, therefore, benefit from producing elongate and smaller spores, that are better suited for wind dispersal, at least at low wind speeds (Ingold, 1965; Gregory, 1973), and are more economic to produce. At higher wind speeds, size is obviously the decisive trait affecting dispersal, whereas spore shape shows no effects (Norros, 2013; Norros et al., 2014).

Previous studies have supported that the above mentioned difference in trophic strategy is reflected in spore morphology: (i) It has been shown that spores of ectomycorrhizal species are larger and more spherical compared to saprotrophic species, though these differences are lineage dependent (Bässler et al., 2015; Andrew et al., 2016). (ii) These observed differences translate into assemblages in the sense that mean spore size of ectomycorrhizal assemblages is larger and mean spore shape more spherical than those of saprotrophic assemblages. Finally, we have indications that, compared to a representative species pool from central and northern Europe, mean spore sizes of assemblages of both guilds are smaller in the Bavarian Forest, a boreal/sub-alpine mountainous area in Germany (Timling and Taylor, 2012; Bässler et al., 2015). At the same time, ectomycorrhizal spores are more spherical, and spores of saprotrophic agarics more elongate (Bässler et al., 2015). The latter response clearly points at a dispersal- and establishment-related phenomenon, which is likely to be more pronounced for fungal assemblages in low-productivity settings (depleted and more patchily distributed resources) for both guilds (Gregory, 1966; Cooke and Whipps, 1993). Low productivity settings are characterised by lower stand density and thus a lower density of roots for ectomycorrhizal fungi to become established, because aboveground biomass is largely correlated with belowground biomass (Vogt et al., 1987). Furthermore, low productivity settings are often accompanied by lower dead organic matter content (Elling et al., 1987; Hoffmann et al., 2014), the basic resources needed by saprotrophic fungi. On the other hand, climate-controlled low productivity areas can accumulate litter and humus which, however, is often related to a lower nutrient (nitrogen) availability due to low turnover (Thomas and Packham, 2007). Both factors contribute to make resources needed by fungi more patchy and unpredictable, even if some specialists seem to have developed endophytic strategies to overcome establishment constraints (see e.g. Parfitt et al., 2010).

To test for the response of the mean spore traits of ectomycorrhizal and saprotrophic assemblages we used data from 48 plots along an elevational gradient in the Bavarian Forest characterised by a steep gradient of resource availability (decrease of host tree density and organic matter, Elling et al., 1987; Heurich and Neufanger, 2005), mainly driven by climate factors (see also Bässler et al., 2016a). If dispersal and establishment are the prevailing selective forces, we expect both guilds to have a decreasing mean spore size and a trend towards elongate spores with a gradient of decreasing resource availability.

## 2. Methods

### 2.1. Fungal and environmental data

To analyse patterns of reproductive traits of fungal assemblages, we sampled macrofungi across a resource depletion gradient (decreasing productivity) in the Bavarian Forest National Park in south-eastern Germany (48°54'N, 13°29'E, see Bässler et al., 2016a for more detail). The Bavarian Forest lies in the south-western part of the Bohemian Massif, which is formed of granite and gneiss. Acidic sand and loamy soils prevail. Elevations range between 650 and 1350 m a.s.l. At 650 to 1150 m a.s.l., forests are dominated by Norway spruce (*Picea abies*) admixed with European beech (*Fagus sylvatica*) and silver fir (*Abies alba*). Above this elevation, forests are dominated by Norway Spruce and Mountain Ash (*Sorbus aucuparia*). This area is characterised by boreal to alpine climate conditions (Walentowski et al., 2004). At higher elevations, mean annual temperature regularly drops below 3.5 °C. As a result, net primary production decreases with elevation; the growing stock of the living stand decreases from approximately 350 to 150 m<sup>3</sup> ha<sup>-1</sup> (Heurich and Neufanger, 2005).

From 2009 to 2011, we sampled soil and litter agaricoid basidiomycetes within 48 circular plots (referred to as the 'local species pool' hereinafter) covering the available elevational gradient in stands dominated by mature spruce. Plots had an area of 200 m<sup>2</sup> and were surveyed at weekly intervals between June and November, i.e. during the main period of fruit body production in the study region. We counted fruit bodies at the species level and removed all fruit bodies from the plots after each survey. All recorded species are included in a data base of ~700 taxa representing the regional species pool of central and northern Europe extracted from Funga Nordica (Knudsen and Vesterholt, 2012; Bässler et al., 2015). For all species information on trophic strategy, fruit body size, spore length and spore width are available (Bässler et al., 2015). Across the regional species pool, the distribution of the mean spore length and width is skewed (Bässler et al., 2015). Therefore, both measures were log<sub>10</sub>-transformed for subsequent statistical analyses. Since these transformed measures are not independent from each other (Bässler et al., 2015), both variables were subjected to a principal component analysis (PCA) on the covariance matrix of log<sub>10</sub>-transformed values, and the scores of the first component (85% explained variance) were used as a measure for spore size and the scores of the second axis (15% explained variance) as a measure for spore shape independent of spore size. Large values of PC1 indicate large spores and large values of PC2 indicate more elongated spores.

To test our hypothesis, we derived a measure of resource depletion. We define resource depletion as the inverse variable of resource availability. Resource availability for fungi is closely correlated with net primary productivity (Carlile et al., 2001). However, direct estimates of net primary productivity for our area were not available. Nevertheless, net primary productivity is strongly correlated with aboveground biomass, which is estimated by the volume of growing stock of forests (m<sup>3</sup> ha<sup>-1</sup>) (Kimmins, 2002). We, therefore, measured the following growing stock variables on the study plots: number of trees, volume (m<sup>3</sup>), basal area (m<sup>2</sup>) and mean diameter at breast height (DBH). To estimate these variables, we used full-wave LiDAR data from airborne laser scanning (Riegl LMS Q-560 system at a point density of 25 points m<sup>-2</sup>) within circular plots of 0.1 ha at the centre of the plots used for sampling fungi. For final analysis, all values were expressed on a 1 ha basis. Laser scanning data allows discrimination between broad-leaved and coniferous tree species and derivation of measures such as the height (m) and DBH (m) of each tree from the laser point clouds (Yao et al., 2012). From the height and DBH

**Table 1**

Results of linear models to test the importance of resource depletion and age of the stand on reproductive characteristics of saprotrophic (Sap) and mutualistic ectomycorrhizal (ECM) fungi. Variance was weighted within the models based on the guild to account for within-group heteroscedasticity. For all comparisons among the models, we used standardized effect sizes (SES) of the parameter estimates using an expected mean of 0 (z-values = estimates divided by the respective standard error). Significant effect sizes are in bold (\*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001). Significant differences (interaction) between the guilds are shaded grey.

	Resource depletion		Age		Fruit body size		Adj. R <sup>2</sup>	
	ECM	Sap	ECM	Sap	ECM	Sap	ECM	Sap
Mean spore size	2.37*	-0.24	0.38	-2.11*	0.64	-3.21**	0.11*	0.23***
Mean spore shape	2.90**	3.54***	2.88**	-0.05	-2.70**	-5.65***	0.53**	0.62***
SES-Local: spore size	2.23*	-0.23	0.50	-2.22*	0.62	-1.20*	0.09*	0.14**
SES-Local: spore shape	3.29**	3.65***	3.02**	-0.17	-2.81**	-5.27***	0.57***	0.60***
SES-Regional: spore size	2.46*	-0.20	0.67	-1.97	0.73	-3.33**	0.12*	0.24***
SES-Regional: spore shape	5.10***	3.51***	3.29**	-0.24	-1.82	-3.66***	0.62***	0.49***

measures, the volume (m<sup>3</sup>) of each tree within a sample plot was calculated using indices that consider the decrease in diameter with tree height according to (Heurich, 2008). The algorithms used to derive these variables were developed, calibrated and validated within our study area (for more details see Heurich, 2008; Yao et al., 2012). We also visually estimated the vegetation cover on each plot (0.02 ha): % cover of shrub layer (>1–5 m), lower tree layer (>5–15 m), and upper tree layer (>15 m). We considered the age of the stand of the plots based on tree ring analysis from forest inventories (Heurich and Neufanger, 2005). Variables such as growing stock, mean DBH and canopy cover are often closely correlated. We, therefore, subjected all variables to a principle component analysis (PCA) based on the correlation matrix. The first component accounted for 52% of the total variance; volume of the growing stock (m<sup>3</sup> ha<sup>-1</sup>) had the highest loading on this component (0.471). Basal area, mean DBH and upper tree layer were also closely correlated with the first component ( $r \approx 0.90$ ). The second component accounted for 17% of the variability; the lower tree layer and forest age showed the highest loadings on this component. By multiplying the first component by minus one, we used the scores of the first component as a measure of resource depletion (large scores indicate a high level of depletion) and the second component as a covariate representing forest stand age (large scores indicate old forest stands; note that 88% of all plots are characterised by stands with a mean age of  $\geq 70$  y).

## 2.2. Statistical analyses

We first divided the data set according to the trophic guilds and calculated the (raw) mean spore size and mean shape for each plot representing an assemblage. We considered only species that occurred at least on four plots to obtain a robust measure of the mean spore dimensions for each assemblage (Bässler et al., 2016a). To control for confounding factors in assembly processes along the resource gradient, we additionally used a null model approach. Thus, effects of co-varying factors in assembly formation, such as species richness patterns, which may obscure the effects we are looking for (mean trait values of assemblages), were excluded (Zelený and Schaffers, 2012). For further details see Bässler et al. (2016a).

We first constructed a local null model that randomises species occurrence across sites but fixes both marginal sums for sites (i.e. species richness of sites) and marginal sums for species (i.e. occupancy of plots across all 48 plots). We first divided the data set according to the trophic guilds and calculated the observed mean size and shape for each plot. We then randomised the community data matrix 1000 times for each guild with the independent swap algorithm (Gotelli, 2000). For each randomised community matrix we calculated the mean spore size as well as the mean shape of spores of the randomised assemblages. Finally, we calculated the

standardised effect size by subtracting the expected mean (mean across all randomisations) from the observed mean and dividing the difference by the standard deviation across the randomisations for each plot.

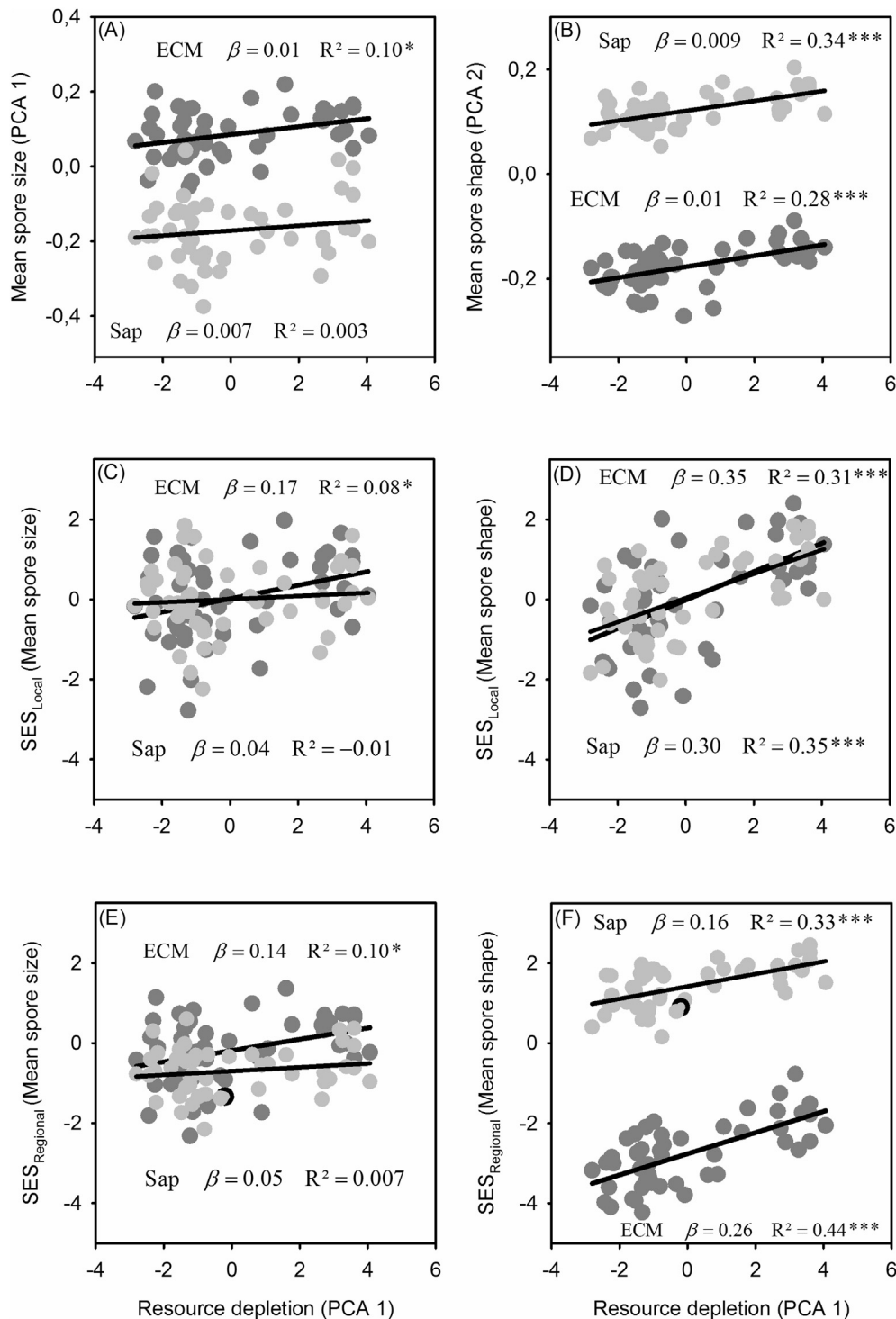
For comparison of local assemblages with the regional species pool, we constructed a second regional null model. We divided the data set according to the trophic guilds as described above. Subsequently, we randomly selected the same number of species as observed for each assemblage and guild from the regional species pool and calculated mean spore size and shape. We repeated this procedure 1000 times for each plot and calculated the standardised effect size by subtracting the expected mean from the observed mean and dividing the difference by the standard deviation across the random draws for each plot. Note that this null model simply tests whether the species recorded in the investigated plots produce spores that differ in size and shape from what would have been expected if species were recruited randomly from the regional species pool.

We finally used the derived response variables (raw mean spore size, raw mean shape, and the standardised effect sizes derived from the local and regional null models of the fungal assemblages) to test for the influence of resource depletion (first principal component) considering the covariate age of the stand (second principal component) by applying generalised least-squares models using the add-on package nlme in R (RDevelopmentCoreTeam, 2013). Variance was weighted within the models based on the guild using the varIdent function (form = ~1|guild) to account for within-group heteroscedasticity structure (Pinheiro and Bates, 2000). For all comparisons among the models, we used standardised effect sizes of the parameter estimates using an expected mean of 0 (z-values = estimates divided by the respective standard error; see Bring, 1994). Since mean spore traits are assumed not to be independent from mean fruit body size (Bässler et al., 2015), we used this measure as covariable in all models.

## 3. Results

During the field studies, 259 species were recorded, of which 40% were saprotrophic, and 60% ectomycorrhizal (for more details and descriptive data see Bässler et al., 2016a).

The effects we found along the resource depletion gradient confirmed our expectations for spore length, but not for volume (Table 1, Fig. 1). We found strong signals in both guilds with mean shape of assemblages changing towards elongation in limited habitats (scatterplot b; line 2/Resource depletion, Table 1). Unexpectedly, mean spore size increased significantly in resource-limited habitats in ectomycorrhizal assemblages (scatterplot e; line 1/Resource depletion, Table 1), independent of mean fruit body size. Finally, spores of ectomycorrhizal assemblages became



**Fig. 1.** Raw scatterplots and linear regressions of (A) mean spore size, (B) mean spore shape, (C, D) standardised effect sizes (SES) of mean spore size and shape (local null model), (E, F) SES of mean spore size and shape (regional null model) compared to resource depletion (first axis of the PCA; see Material and methods for details). Light grey symbols: saprotrophic fungi; dark grey symbols: ectomycorrhizal fungi. Slopes ( $\beta$ ) and adjusted  $R^2$  from univariate linear regression models are given. Significance levels: 0.05\*, 0.01\*\*, 0.001\*\*\*.

particularly elongated in older stands, and spore size of saprotrophic assemblages somewhat smaller (line 2/Age, Table 1). The two null models confirmed that the signals were consistent, and that the raw turnover in spore traits along both the resource and the stand age gradient, was not reflecting random species assembly, neither from the regional, nor from the local species pool (Table 1).

#### 4. Discussion

The strong increase in spore elongation along the resource depletion gradient supports our hypothesis that dispersal fitness becomes increasingly important for both guilds under resource constraints and patchy distribution. Oblong spores are carried

further by air movement (see Introduction). At the same time it is self-evident that for a given hymenial surface, more spores can be produced, because elongate spores, of the same volume as more spherical spores, allow denser packing (Halbwachs and Bässler, 2015). Although ectomycorrhizal spores became more elongate along the resource depletion gradient, it should not be regarded as contradictory that these spores are on average more spherical in the local species pool than in the regional pool. Even at the high level of sphericity found (see Fig. 1), ectomycorrhizal spores showed a clear signal of increasing elongation with resource depletion. However, there seems to be a trade-off between dispersal and susceptibility to microbial attacks, because the more spherical a spore is shaped, the less surface is exposed per volume (Bässler et al., 2015; see Table S1). This is in line with the fact that ectomycorrhizal spores need to survive until conditions for root colonisation are suitable (Halbwachs and Bässler, 2015).

Fragmented resource patterns lead to colonisation constraints that can be compensated by more effective dispersal (Pickett and White, 1985). It has been suggested that in agaricoid basidiomycetes, wind is one of the most important agents responsible for dispersal (Halbwachs and Bässler, 2015 and references therein). Dispersal should become more important than competition when resources are fragmented. Thus, dispersal affects assemblage composition, as multiple lines of evidence of island biogeographical studies suggest (Peay et al., 2007). Our results support the initial assumption that productivity is correlated with dispersal fitness of assemblages.

The spore size increase for ectomycorrhizal agarics with resource depletion comes as a surprise as we expected to find a decrease in mean spore size with resource depletion if dispersal capability is the most important driver. On the other hand, this response may be a trade-off between dispersal fitness and survivability, since ectomycorrhizal in contrast to saprotrophic spores rely on prolonged survivability to get access to host roots (see Introduction). Equally surprising, mean spore size of saprotrophs was not affected along the resource gradient, whereas we expected that they would become smaller, to boost dispersal fitness. Saprotrophic spore size became smaller solely with stand age, though only to a minor extent and with low significance. Spores of saprotrophs are generally smaller than those of ectomycorrhizal fungi and based on the null model approach we showed that our assemblages had significantly smaller spores than species in the regional species pool (see Fig. 1A and Bässler et al., 2015). This indicates that the studied saprotrophic assemblages are skewed towards a lower limit in sexual spore size. We speculate that saprotrophic spores cannot become much smaller to improve dispersal, because this would lose too much germination competence. Successful germination depends on sufficient internal water and carbon reserves (Gottlieb, 1966). In contrast, ectomycorrhizal fungi possess more options to optimise spore dispersal. In particular, they can invest in higher spore numbers at the same time producing larger spores, because they generally have larger fruit bodies than saprotrophs (Bässler et al., 2015). At least in theory, this could limit the trade-off between spore size and numbers that appear prevalent among saprotrophic fungi.

We finally need to add a cautionary note. Most studies using elevational gradients face the problem of co-varying variables, and, therefore, confounding effects (Körner, 2007). In our setting, not only is resource depletion correlated with elevation, but so also are climate variables, such as temperature and precipitation (see Table S2 and Bässler et al., 2016b). We are aware that both resource depletion and climate might contribute to explain the pattern observed in our study. However, here we present some arguments for why it is more probable that, in our setting, climate acts mainly indirectly via resource availability, and not directly on the mean

traits of assemblages. A previous study hypothesised that spore size is related to the availability of water. Water storage in spores has been interpreted as a critical factor for successful germination of primary mycelia in drier micro-environments (Kausserud et al., 2010). However, water is not a limiting factor in our study area which is characterised by a high level of moisture and humidity throughout the year along the whole elevational gradient (see Bässler, 2004; Bässler et al., 2016a). Furthermore, although temperature correlates with metabolic rate, especially in ectothermic organisms, hence with growth speed of fungi (Cooke and Whipps, 1993), a direct effect on spore traits has so far been neither shown nor hypothesised. To the best of our knowledge, reasonable physiological principles and assumptions are so far lacking. Taken together, we suggest that most of the variation in mean spore traits of the assemblages in our study can be attributed to the gradient of resource depletion, derived from basic ecological principles.

## 5. Conclusion

The strong response of mean spore traits of assemblages along the resource gradient, found by our study, supports our assumption that dispersal and establishment fitness is ecologically highly relevant under resource constraints, because it seems to be an important driver in assembly processes for both guilds.

However, our interpretations of the drivers behind observed patterns are, to some extent, speculations, and we are far from completely understanding the role of size and shape in fungal spores under resource and climate constraints. To further clarify the ecological relevance of our findings, we propose to analyse broader data sets across non-agaricoid guilds. This should include trait reconstruction across other fungal phyla and by applying genomics and transcriptomics for elucidating the evolution of spore morphology. Finally, we suggest investigating spore traits along artificially created resource gradients, that are not co-varying with climate.

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## Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.funeco.2016.12.001>.

## References

- Andrew, C., Heegaard, E., Halvorsen, R., Martínez-Peña, F., Egli, S., Kirk, P.M., Bässler, C., Buntgen, U., Aldea, J., Høiland, K., 2016. Climate impacts on fungal community and trait dynamics. *Fungal Ecol.* 22, 17–25.
- Bässler, C., Halbwachs, H., Karasch, P., Holzer, H., Gminder, A., Kriegelsteiner, L., Gonzalez, R.S., Müller, J., Brandl, R., 2016a. Mean reproductive traits of fungal assemblages are correlated with resource availability. *Ecol. Evol.* 6, 582–592.
- Bässler, C., Müller, J., Cadotte, M.W., Heibl, C., Bradtka, J.H., Thorn, S., Halbwachs, H., 2016b. Functional response of lignicolous fungal guilds to bark beetle deforestation. *Ecol. Indic.* 65, 149–160.
- Bässler, C., 2004. Das Klima im Nationalpark Bayerischer Wald - Darstellung, Entwicklung und Auswirkung. Nationalparkverwaltung Bayerischer Wald, Grafenau, Germany.
- Bässler, C., Heilmann-Clausen, J., Karasch, P., Brandl, R., Halbwachs, H., 2015. Ectomycorrhizal fungi have larger fruit bodies than saprotrophic fungi. *Fungal Ecol.* 17, 205–212.
- Boberg, J.B., Näsholm, T., Finlay, R.D., Stenlid, J., Lindahl, B.D., 2011. Nitrogen availability affects saprotrophic basidiomycetes decomposing pine needles in a long term laboratory study. *Fungal Ecol.* 4 (6), 408–416.
- Bring, T., 1994. How to standardize regression coefficients. *Am. Statistician* 48,

- 209–213.
- Brundrett, M.C., 1991. Mycorrhizas in natural ecosystems. In: Begon, M., Fitter, A.H., Macfadyen, A. (Eds.), *Advances in Ecological Research* 1991, vol. 21. Academic Press, London, pp. 171–313.
- Bruns, T.D., Peay, K.G., Boynton, P.J., Grubisha, L.C., Hynson, N.A., Nguyen, N.H., Rosenstock, N.P., 2009. Inoculum potential of *Rhizopogon* spores increases with time over the first 4 yr of a 99-yr spore burial experiment. *New Phytol.* 181, 463–470.
- Carlile, M.J., Watkinson, A.C., Gooday, G.W., 2001. *The Fungi*. Academic Press, p. 588.
- Cooke, R.C., Whipps, J.M., 1993. *Ecophysiology of Fungi*. Blackwell Scientific Publications.
- Elling, W., Bauer, E., Klemm, G., Koch, H., 1987. Klima und Böden - Waldstandorte. Schriftenreihe des Bay. Staatsmin. Ern. Land. Und Forsten 1.
- Fries, N., Bardet, M., Serck-Hanssen, K., 1985. Growth of ectomycorrhizal fungi stimulated by lipids from a pine root exudate. *Plant Soil* 86 (2), 287–290.
- Gotelli, N.J., 2000. Null model analysis of species cooccurrence patterns. *Ecology* 81, 2606–2621.
- Gottlieb, D., 1966. Carbohydrate metabolism and spore germination. In: Madelin, M. (Ed.), *The Fungus Spore*. Butterworths, London, pp. 141–163.
- Grayston, S.J., Vaughan, D., Jones, D., 1997. Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. *Appl. Soil Ecol.* 5, 29–56.
- Gregory, P., 1966. The fungus spore: what it is and what it does. In: Madelin, M. (Ed.), *The Fungus Spore*. Butterworths, London, pp. 1–13.
- Gregory, P.H., 1973. *Microbiology of the Atmosphere*, second ed. John Wiley & Sons, New York.
- Halbwachs, H., Bässler, C., 2015. Gone with the wind – a review on basidiospores of lamellate agarics. *Mycosphere* 6, 78–112.
- Heurich, M., 2008. Automatic recognition and measurement of single trees based on data from airborne laser scanning over the richly structured natural forests of the Bavarian Forest National Park. *For. Ecol. Manag.* 255, 2416–2433.
- Heurich, M., Neufanger, M., 2005. Die Wälder des Nationalparks Bayerischer Wald. *Wiss. Reihe Des. Natl. Bayer. Wald* 16. Grafenau.
- Hoffmann, U., Hoffmann, T., Jurasinski, G., Glatzel, S., Kuhn, N., 2014. Assessing the spatial variability of soil organic carbon stocks in an alpine setting (Grindelwald, Swiss Alps). *Geoderma* 232, 270–283.
- Ingold, C.T., 1965. *Spore Liberation*. Clarendon Press. Oxford University Press, Oxford.
- Kauserud, H., Heegaard, E., Halvorsen, R., Boddy, L., Høiland, K., Stenseth, N.C., 2010. Mushroom's spore size and time of fruiting are strongly related: is moisture important? *Biol. Lett.* 7 (2), 273–276.
- Kikuchi, K., Matsushita, N., Suzuki, K., Hogetsu, T., 2007. Flavonoids induce germination of basidiospores of the ectomycorrhizal fungus *Suillus bovinus*. *Mycorrhiza* 17, 563–570.
- Kimmins, J.P., 2002. *Forest Ecology*, third ed. (Benjamin Cummings).
- Kirk, P.M., Cannon, P.F., Minter, D.W., Stalpers, J.A., 2011. *Ainsworth & Bisby's Dictionary of the Fungi*, tenth ed. Cabi Publishing.
- Knudsen, H., Vesterholt, J., 2012. *Funga Nordica: Agaricoid, Boletoid, Clavarioid, Cyphelloid and Gastroid Genera*. Nordsvamp.
- Körner, C., 2007. The use of 'altitude' in ecological research. *Trends Ecol. Evol.* 22 (11), 569–574.
- Lindahl, B., Boberg, J., 2008. Distribution and function of litter basidiomycetes in coniferous forests. In: Boddy, L., Frankland, J.C., van der West, P. (Eds.), *Ecology of Saprotrophic Basidiomycetes*. Academic Press, pp. 183–209.
- Nara, K., 2009. Spores of ectomycorrhizal fungi: ecological strategies for germination and dormancy. *New Phytol.* 181, 245–248.
- Nguyen, N.H., Hynson, N.A., Bruns, T.D., 2012. Stayin' alive: survival of mycorrhizal fungal propagules from 6-yr-old forest soil. *Fungal Ecol.* 5, 741–746.
- Norros, V., 2013. *Measuring and Modelling Airborne Dispersal in Wood Decay Fungi*. doctoral thesis. University of Helsinki, Helsinki.
- 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.
- Osono, T., 2003. Effects of prior decomposition of beech leaf litter by phyllosphere fungi on substrate utilization by fungal decomposers. *Mycoscience* 44, 41–45.
- Parfitt, D., Hunt, J., Dockrell, D., Rogers, H.J., Boddy, L., 2010. Do all trees carry the seeds of their own destruction? PCR reveals numerous wood decay fungi latently present in sapwood of a wide range of angiosperm trees. *Fungal Ecol.* 3 (4), 338–346.
- Peay, K.G., Bruns, T.D., Kennedy, P.G., Bergemann, S.E., Garbelotto, M., 2007. A strong species–area relationship for eukaryotic soil microbes: island size matters for ectomycorrhizal fungi. *Ecol. Lett.* 10, 470–480.
- Perrin, N., 2009. Dispersal. In: Levin, S.A. (Ed.), *The Princeton Guide to Ecology*. Princeton University Press, Princeton & Oxford, pp. 45–50.
- Pickett, S.T.A., White, P.S., 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press.
- Pinheiro, J.C., Bates, D.M., 2000. *Mixed-effects Models in S and S-PLUS*. Springer, New York.
- Pringle, A., Vellinga, E., Peay, K., 2015. The shape of fungal ecology: does spore morphology give clues to a species' niche? *Fungal Ecol.* 17, 213–216.
- RDevelopmentCoreTeam, 2013. R: A language and environment for statistical computing from.** <http://www.R-project.org>.
- Reid, N., 1991. Coevolution of mistletoes and frugivorous birds? *Aust. J. Ecol.* 16, 457–469.
- Spooner, B.M., Roberts, P.J., 2005. *Fungi* (Harper UK).
- Thomas, P., Packham, J., 2007. *Ecology of Woodlands and Forests: Description, Dynamics and Diversity*. Cambridge University Press.
- Timling, I., Taylor, D.L., 2012. Peeking through a frosty window: molecular insights into the ecology of Arctic soil fungi. *Fungal Ecol.* 5, 419–429.
- Vogt, K.A., Vogt, D.J., Moore, E.E., Fatuga, B.A., Redlin, M.R., Edmonds, R.L., 1987. Conifer and angiosperm fine-root biomass in relation to stand age and site productivity in Douglas-fir forests. *J. Ecol.* 857–870.
- Walentowski, H., Ewald, J., Fischer, A., Kölling, C., Türk, W., 2004. *Handbuch der natürlichen Waldgesellschaften in Bayern (Geobotanica, Freising)*.
- Willson, M.F., Traveset, A., 2000. The ecology of seed dispersal. In: Fenner, M. (Ed.), *Seeds: the Ecology of Regeneration in Plant Communities*. CABI Publishing International, pp. 85–110.
- Yao, W., Krzystek, P., Heurich, M., 2012. Tree species classification and estimation of stem volume and DBH based on single tree extraction by exploiting airborne full-waveform LiDAR data. *Remote Sens. Environ.* 123, 368–380.
- Zelený, D., Schaffers, A.P., 2012. Too good to be true: pitfalls of using mean Ellenberg indicator values in vegetation analyses. *J. Veg. Sci.* 23, 419–431.