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Small can be beautiful: Ecological trade-offs related to basidiospore size

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Abstract

Investments of Agaricomycetes in morphological reproductive traits are constrained by a limited energy budget, as in any other fungal group. Such investments relate to fruit body size and number, and to spore size, the latter which is correlated with nutrient reserves. These ecological trade-offs are indicators of fungal lifestyles, for example ruderal vs competitive strategies. To shed some light on morphological trade-offs, we looked into pertinent correlations by comparing datasets about relative fruit body dry weights with fruit body and spore size, and fruit body number with fruit body size. In addition, we demonstrated how spore size translates to investments into nutrient reserves. We could confirm results from earlier studies which showed a positive correlation between fruit body and spore size, as well as a negative correlation between fruit body number and size. Finally, we found weak, but highly significant trade-offs between dry matter content of trama and total spore volume per hymenal area unit. In conclusion, we pointed to the fact that only considering reproductive morphological trade-offs would fall short of the complex morphological and physiological interrelationships in fungal individuals (genets). The need for further studies to gain a more comprehensive picture of input-output trade-offs would be the logical consequence.

Key words – energy budget – fruit body size and number – metabolic competence – secondary metabolites – spore size and nutrient reserves

Introduction

Macrofungi are important agents in ecosystems. Saprotrophic fungi primarily recycle plant biomass, and ectomycorrhizal species are indispensable as symbionts of woody plants (Moore et al. 2011). Therefore, a deeper, mechanistic understanding of their functions will help understand ecosystems. Fungal traits allow such insights. In macrofungi, fruit bodies are an outstanding feature, serving as organs for reproduction and dispersal by spores (Dix & Webster 1995). In this study, we focus on basidiospores of stipitate Agaricomycetes.

Apart from showing a wide spectrum of pigmentation and shape, basidiomycetes exhibit a remarkable intra- and interspecific variation in mean fruit body biomass, spore size and spore number (Halbwachs & Bässler 2015, Halbwachs et al. 2016), traits that are related to investments in reproduction and dispersal (Cooke & Whipps 1993).

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For example, fruit body biomass is likely to be correlated with longevity, and spore size to germination potency (Halbwachs & Bässler 2015, Halbwachs et al. 2016). There are indications that genets of taxa with small fruit bodies produce more fruit bodies than those with large ones, a trend which indicate differential lifestyles, i.e. ruderal and competitive (r- and K-selected, Andrews 1992), especially under resource limitation (Bässler et al. 2016).

Basidiospore traits also reflect r- and K-selected lifestyles. Gregory (1966) coined the terms xeno- and memnospores. The former are small, travel further and germinate more readily than the latter, which tend to be larger and can survive longer under unfavourable conditions (Table 1). The more effective air dispersibility of smaller spores has been confirmed by Norros et al. (2014).

Table 1 Characteristics of small and large fruit bodies and basidiospores

	Longevity	**Life strategy**	**Dispersal type**
Large basidiospore	Long-lived	K-selected	Memnospore
Small basidiospore	Short-lived	r-selected	Xenospore
Large fruit body	Long-lived	K-selected	
Small fruit body	Short-lived	r-selected	

Physiological characteristics, such as texture of fruit bodies, should certainly have an ecological meaning because reinforcing hyphal structures require extra investments. These investments include above all modifications of fruit body trama, for instance densely packed generative hyphae with no or few air-filled spaces, thick-walled generative hyphae (supporting hyphae), and thick-walled, turgid fusiform hyphae (physalohyphae) (see Clémençon et al. 2012). Such architectural trama improvements lead to robust and long-lived fruit bodies.

Since the specific energy budget of a species is restricted by the characteristics of its niche (Kearney et al. 2010), investments into fruit body number, size and texture or into spore size and number require counterbalances (ecological tradeoffs, Wikelski 2009) (Table 2).

Table 2 Hypothetical trade-offs of Agaricomycete reproductive organs

Primary investment	**Trade-off**
Large spores	– Few spores
Many fruit bodies	– Small, short-lived fruit bodies
	– Small spores
Tough fruit body texture	– Small fruit bodies
	– Small spores

In this study, we endeavoured to elucidate these trade-off possibilities by exploring data about spore volume geometry, and the relationship between fruit body texture, biomass and spore size.

Materials & Methods

Mean fruitbody diameter and mean spore dimensions we extracted from the Funga Nordica (Knudsen & Vesterholt 2012) and other fungas (Smith & Singer 1964, Moser 1983, Ludwig 2001-2017). The squared fruit body diameter we used as proxy for biomass (Tóth & Feest 2007). Spore dimensions were used to calculate the ellipsoidal volumes.

To show the effect of spore size on the investment in potential spore nutrient reserves, we selected eleven exemplary species with ±globose spores with differing spore diameters and calculated the total of spore volume per mm^2 hymenal surface area.

To model a possible correlation between fruit body number and spore size, we used a dataset from the Bavarian Forest (Germany) containing reproductive traits of 259 Agaricomycetes. We fitted the log-normalised data to a linear model (“Least Square Regression”) that is robust to outliers by using "Least Trimmed Squares", and calculated the coefficient of determination together with significance levels p (permutation test with 9,999 replicates) using "PAST 3.14" (Hammer 2016).

As a proxy for the mass of reinforcing trama hyphae, we determined the fresh: dry weight ratio of 461 Agaricomycetes. We first collected vital samples (mean n=6.4) of 74 stipitate species from sites in Liguria/Italy (44°22'N 9°37'E) and northern Bavaria/Germany (49°35'N 9°12'E), and dried them for 48 hrs at 40°C (Halbwachs 2018). Fresh and dried specimen were weighted using a Steinberg SBS-LW Balance (accuracy ± 1 mg). In addition, we used 350 datasets of macrofungi collected in Finland (Ohenoja et al. 1993), and 47 datasets from Kalač (2016), Zellner (1907). This data base, complemented by mean fruit body and spore sizes, we then subjected to the same statistical procedure as mentioned before.

Results

Spore nutrient reserve volumes

This fundamental relationship shows a decreasing production of spore contents including nutrient reserves per hymenal area unit with decreasing spore diameter (Fig. 1).

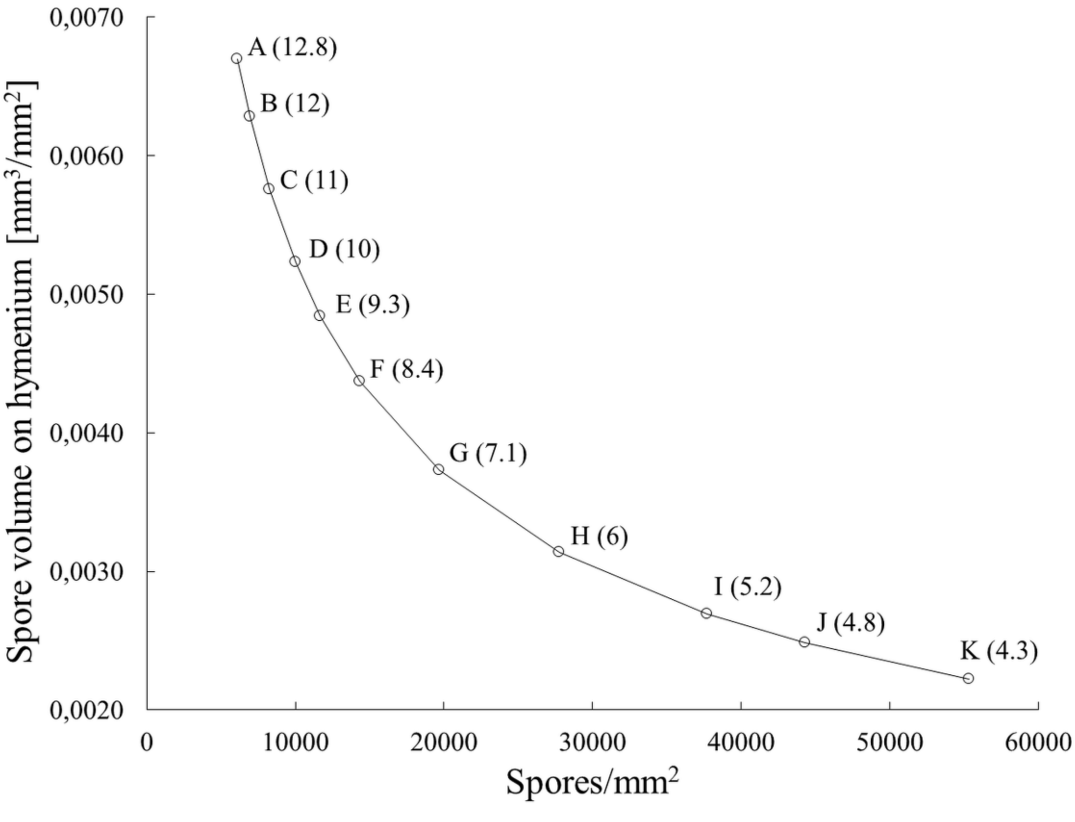

Fig. 1 – The 11 Agaricomycetes show a cubic function between spore diameter (µm in brackets) and spore volume. A *Laccaria tortilis*. B *Amanita submembranacea*. C *Entoloma saundersii*. D. *Fayodia bisphaerigera*. E *Mycena clavularis*. F *Coprinopsis spilospora*. G. *Lactarius picinus*. H *Hydropus floccipes*. I *Lyophyllum paelochroum*. J *Camarophyllopsis micacea*. K *Clitocybe globispora* (Species names according to IndexFungorum.org).

Fruit body number vs fruit body and spore size

We found a weak but significant negative correlation between fruit body number and spore size ($r^2 > 0.03$, $p < 0.005$) as well as between fruit body number and biomass ($r^2 = 0.078$, p =0, 0001). These trends confirm similar results of Bässler et al. 2015, 2016.

Fruit body texture vs fruit body and spore size

Increasing % dry weight did only weakly but significantly correlate negatively with fruit body size ($r^2 = 0.012$, $p < 0.02$). % dry weight vs spore size of saprotrophic Agaricomycetes showed a larger and highly significant signal ($r^2 = 0.06$, $p < 0.002$) (Fig. 2). Ectomycorrhizal species did not show such a relationship.

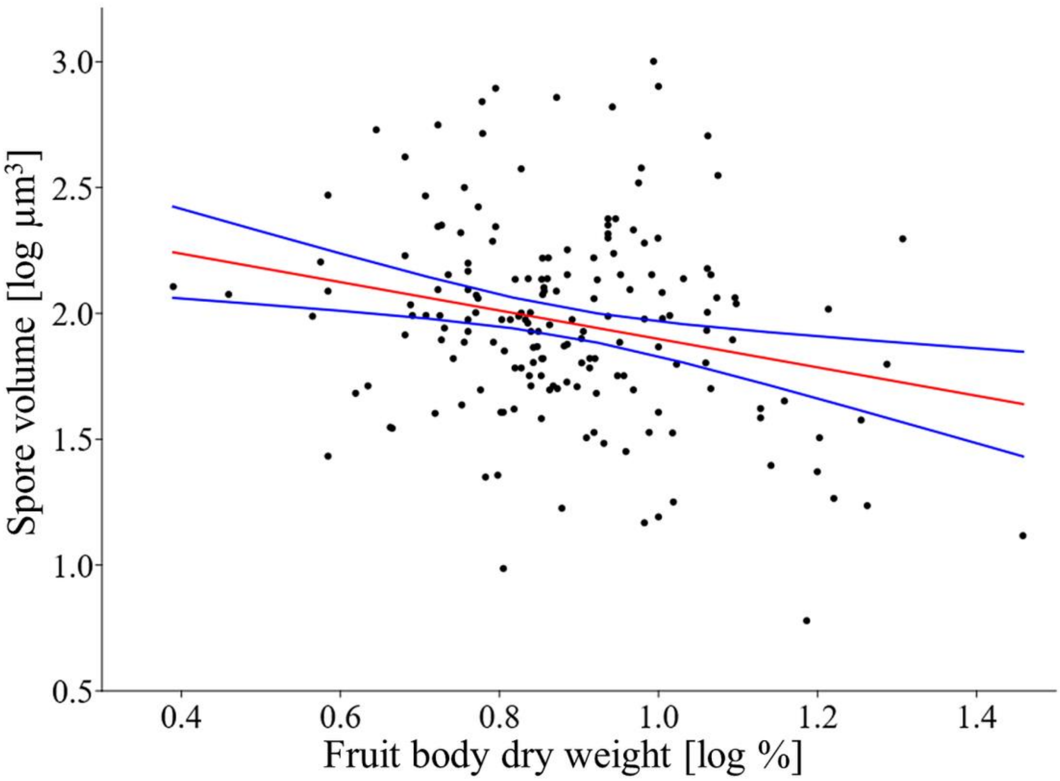

Fig. 2 – Scatterplot of the regression between % dry fruit body matter and spore size for saprotrophic Agaricomycetes. The blue lines delineate the upper and lower 95% confidence limits.

Discussion

Spore nutrient reserves

It may seem trivial to present a simple spherical calculation to show the effect of spore diameter on spore volume. Nevertheless, to our knowledge, this is the first time that this is highlighted in a study (or textbook). The implications are obvious with regard to costly spore contents, above all nutrient reserves. Basidiospores require high-quality nutrients for dormancy (longevity) and germination, especially lipids and carbohydrates (Allen 1965, Cochrane 1974, Weete 1981). Data on the proportions of these nutrients in basidiospores are scarce. The lipid content seems to range between 13% and 30% (mean 20%) (Tulloch & Ledingham 1962, Sumner 1973, Weete & Kelley 1977, Taber & Taber 1982, Tereshina et al. 2007). The carbohydrate content amounts e.g. to 12% in *Agaricus bisporus* and 15% in *Flammulina velutipes* (Tereshina & Memorskaya 2005, Tereshina et al. 2007). It should be noted that the energy density of lipids is 2.5 times as high as of carbohydrates (www.nal.usda.gov/fnic).

Fruit body number vs spore and fruit body size

It came to no surprise that the larger the fruit body number a genet produces the smaller the spore volume because the latter negatively co-varies with fruit body biomass (see also Bässler et al. 2015). These results merely showed a trend towards possible trade-offs, whereby a Principal Component Analysis attributed the highest explanation of variance to fruit body biomass (not shown).

Fruit body texture vs fruit body and spore size

Surprisingly, the signal for texture vs spore volume was 5 times stronger than for texture vs fruit body biomass. This should not be overrated because both coefficients of determination were fairly low. Still, we see a plausible trend, pointing to a trade-off between investments in texture and in biomass. The fact that this correlation is not detectable in the ectomycorrhizal guild may be attributed to the ample and more reliable supply of sugars from the hosts (Corrêa et al. 2011), and to the fact that fruit bodies of ectomycorrhizal species generally have a relatively soft consistency (Simmel & Poschlod 2017).

The bottom line

Although we see some plausible trends as previously predicted (Table 2), clear cut trade-offs have not been found. The throughout relatively low coefficients of determination indicate complex and interrelated causalities. It is a well-known phenomenon also in other scientific fields that deal with complex systems such as social research (Moksony 1999). It appears that there is more to be considered than simply some morphological trade-offs between reproductive structures. Moreover, physiological activities need to be accounted for (Table 3).

Table 3 A compilation of fungal traits (Halbwachs & Bässler 2015, Halbwachs et al. 2016) that require energy input. Green arrows indicate issues treated in this study.

Energy budget	Morphology	Mycelium size	▶	Hyphal biomass
		Mycelial turnover	▶	Autolysis and regrowth
		Fruit bodies per genet and time unit	▶ (green)	Total fruit body biomass
		Fruit body size	▶ (green)	
		Fruit body rigidity, longevity	▶ (green)	Proportion of hyphal stabilisers
		Fruit body cuticle morphology	▶	E.g., gelified, strigose
		Spore size and number	▶ (green)	Total spore biomass
		Storage organs	▶	Sclerotia etc.
	Physiolog	Metabolic competence	▶	Enzymatic pathways, etc.
		Pigments	▶	Protective properties, e.g., of melanins
		Thermal protection	▶	Carbohydrates, lipids, heat shock proteins
		Microbial protection	▶	Antibiotics
		Deterrants, attractants, signalling	▶	Toxins, volatiles, etc.

This compilation gives a good idea how complicated input-output tradeoffs in the lifecycle of Agaricomycetes (and other fungal groups) are. To get a more comprehensive picture, studies about physiological and morphological investments other than reproductive structures need to be launched

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Accessibility of data

Raw data can be provided on request.

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