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# Tales and mysteries of fungal fruiting: How morphological and physiological traits affect a pileate lifestyle

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## ABSTRACT

Mushroom-forming fungi exhibit a tremendous variety of morphological, physiological and behavioural traits. Though science had taken up the challenge to relate these traits to functions in the 20<sup>th</sup> century, such deliberations became much rarer in recent decades. In the review presented here we aim at reviving this research area, particularly in regard to ecological implications. We have therefore compiled fruit body traits with their evidenced or suggested functions. Some traits have no immediate functional meaning, but many are suggestive of some ecological importance. Many traits serve more than one function, and traits interact in the sense of trade-offs, patterns that reflect the economy of fungal design. In conclusion, the review comes up with well and little-known mushroom properties, and the numerous gaps in attributing traits to functions.

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## 1. Introduction

After having spore traits and dispersal-related mechanisms presented in a previous review (Halbwachs and Bässler 2015), we now focus on the fruit bodies traits proper. This encompasses architectural, reproductive, protective, growth- and phenology-related traits.

Functional traits have evolved either by adaptive radiation (Gillespie, 2009) or by exaptation (Gould, 1997). These traits are intricately interrelated to ecological behaviour and fitness (Palm and Chapela, 1997; Violle et al., 2007). Or

in other words, if we want to fully understand the ecology of organisms, populations, ecosystems, and biodiversity patterns a trait-based approach is needed (Koide et al., 2014; Aguilar-Trigueros et al., 2015). In fungi such a methodology has only been applied in few cases (e.g. Bässler et al., 2015, 2016a,b; Halbwachs et al., 2014). Mycological pioneers like A.H.R. Buller or E. Gäumann have tackled in the early 20<sup>th</sup> century some of the more basic questions relating to sporocarps. Some additional answers about fruiting behaviour and fruit body ecology were supplied by e.g. R. Moser and H. Cléménçon during the second half of last century, and

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recently by Bässler *et al.* (2014). Many aspects still remain in the dark, particularly about the connection between ecological strategies of fungi and traits of their fruit bodies (Pringle *et al.*, 2015).

Higher fungi display a striking variety of fruit bodies (Fig. 1).

In this review, we focus on basidiomycete macrofungi that form mushrooms, i.e. agaricoid and boletoid fruit bodies of saprotrophic and ectomycorrhizal fungi. The probably first agaricoid basidiomycete appeared in the evolutionary history of life during the Cretaceous (see Fig. 2), judging by the extremely meagre fossil record (Taylor *et al.*, 2014: 179). The number of mushroom-forming species (agarics and boletes) is presently likely to surpass 9000 world-wide (Kirk *et al.*, 2011). This figure is conservative, because with proliferating application of molecular methods drastic rise of new species is to be expected (Hawksworth, 2001; Blackwell, 2011).

Mushrooms vary in shape, size, longevity, growth habits, phenology, colour, texture, odour, taste and more. These qualities apply to the saprotrophic as well as to the ectomycorrhizal guild. As in other organisms traits and trait combinations (!) should also be adaptive in fungi (Gavrilets and Losos, 2009). There are many widely scattered direct and indirect suggestions and clues in the sense of expert opinions, but only very few that are armed with hard evidence, e.g. the antibiotic pigment in *Mycena aurantiummarginata* (Jaeger and Spiteller, 2010). This is in most cases understandable, because testing e.g. assumptions about the adaptive value of colour or taste is either very difficult or not feasible. For statistical investigations, fungal databases are mostly too limited, particularly with regard to abiotic and biotic circumstances associated with occurrence.

We have, however, compiled all pertinent information about response traits of agaricoid and boletoid basidiomycetes accessible to us and offer either evidenced or plausible explanations whenever possible. The latter should give a kick – so we hope – towards more studies in this research area.

We follow a line which starts with the question why stipitate sporocarps of basidiomycete agarics (Agaricales and Boletales) take a pivotal role in fungal biology in the first place, followed by a detailed account of what mushrooms have morphologically and physiologically developed to optimise their dispersal fitness under differing environmental regimes. We then describe how mushrooms are formed as part of the fungal lifecycle, and round off with looking at the timing of mushroom fruiting (phenology).

As we try to uncover trends, all relative and absolute measures refer to averages, if not stated otherwise. Taxon names have been adopted from [www.speciesfungorum.org](http://www.speciesfungorum.org). Authors of figures are listed in the Appendix Table A2, if not otherwise mentioned in captions. The remaining figures have been contributed by the authors.

## 2. Why fruit bodies?: the ecological rationale of fungal fruiting

Any organism needs to propagate and to disperse. Dispersal is essential for foraging and expanding to additional habitats

(“bet hedging”, see e.g. Mayhew, 2006: 67f), facilitating the reduction of intraspecific competition (Mayhew, 2006: 66), alleviating predation pressure by reducing density (Janzen-Connell hypothesis, see Nathan and Casagrandi, 2004) but also allopatric speciation (Giraud *et al.*, 2010). Higher fungi, being sessile and iteroparous organisms, disperse by vegetative and sexual means.

Fungal fruit bodies produce propagules (diaspores) for sexual propagation. Their haploid germ tubes merge by outcrossing and form dikaryotic mycelia (Carlile *et al.*, 2001: 58, 248). Without sex, higher fungi would be less adaptable to environmental changes and highly variable parasites (Brown, 1999). Heterozygotic outcrossing leading to meiosis also provides means to repair DNA damage (Moore and Frazer, 2002: 68), and to resist cellular parasites through mutations (Hamilton *et al.*, 1990). In addition, sex reduces intraspecific competition by producing genotypic variants (Brown, 1999). Moreover, the genotypic plasticity allows fungi to occupy new habitats more successfully, thus fostering speciation (Mayhew, 2006: 137–142). Obviously, benefits of recombination and investing in fruit bodies evolved because sex pays, though pay-offs are likely (cf. Bonte *et al.*, 2012).

Vegetative propagation is mainly achieved by developing hyphal structures (mycelia, rhizomorphs and sclerotia) that are often capable to bridge considerable distances. Some basidiomycetes grow rhizomorphs over several hundred meters, e.g. *Armillaria bulbosa* during over 1000 y (Anderson, 1992). This exemplifies the major constraint of vegetative propagation. It is slow and cannot react to short term threats, such as long-lasting water logging episodes. Propagation by diaspores overcomes space and time constraints in a far more effective way than vegetative propagation. Dispersal of spores can happen by abiotic mechanisms (mainly by air and water movement), and by biotic vectors such as insects and mammals, bridging distances of several kilometres within few days (Halbwachs and Bässler, 2015). A special case is *Mycena citricolor*, a tiny mushroom parasitising on *Citrus*. Its cap acts itself as diaspore (Watling, 1996).

In agaricoid and boletoid basidiomycetes, diaspores are produced in a hymenium (lamellae or tubes) which is attached to the underside of the cap of a mushroom. In other basidiomycetes the hymenium may rest inside the sporocarp as in gasteroid fungi, cover the ends of coralloid fruit bodies as in *Ramaria* or the whole fruit body as in the Tremellaceae, and may completely cover the surface of corticoid fungi or covers the underside of bracket fungi (cf. Clémenton *et al.*, 2012: 291–301). As we will see in the following sections, the mushroom architecture has many ecological functions and may even have advantages over other fungal blueprints.

## 3. Form follows function: the mushroom blueprint

The basic architecture of agaricoid and boletoid fruit bodies aka basidiomes, basidiocarps, sporocarps or simply mushrooms has not changed probably since approximately 100 million years (Hibbett *et al.*, 1995): stipe, cap, sporophore. This arrangement is obviously successful, and, therefore,

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