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Ectomycorrhizal fungi have larger fruit bodies than saprotrophic fungi

Claus BÄSSLER[a,*], Jacob HEILMANN-CLAUSEN[b], Peter KARASCH[d], Roland BRANDL[c], Hans HALBWACHS[d]

[a]Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany
[b]Centre for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, DK-2100 Copenhagen, Denmark
[c]Animal Ecology, Department of Ecology, Faculty of Biology, Philipps-Universität Marburg, 35037 Marburg, Germany
[d]Bavarian Mycological Society, Danzigerstr. 20, 63916 Amorbach, Germany

ARTICLE INFO

Article history:
Received 5 November 2013
Revision received 30 January 2014
Accepted 17 June 2014
Available online 30 August 2014
Corresponding editor:
Anne Pringle

Keywords:
Dispersal
Reproductive traits
Spore shape
Spore size
Sporocarp
Trade-off
Trophic guilds

ABSTRACT

Currently we have only a limited understanding of the evolutionary and ecological significance of reproductive traits of fungi. We compared data on fruit body size, spore size and shape between saprotrophic and mutualistic (ectomycorrhizal) fungi in Northern and Central Europe. Lifestyle and reproductive traits showed strong phylogenetic signals. A phylogenetically informed analysis demonstrated that saprotrophs produce on average smaller fruit bodies than mutualistic species. The two guilds, however, do not differ in spore size. Overall this suggests that fruit bodies of ectomycorrhizal fungi produce on average more spores than saprotrophic fungi. We argue that this difference is related to resource availability: ectomycorrhizal fungi receive carbon from their hosts and, therefore, evolution favours large fruit bodies, whereas the fruit body size of saprotrophic fungi might have responded to resource availability and the distribution and size of resource patches.

Introduction

Fungi are key players in terrestrial ecosystems (Miller 1995) and play a pivotal role in ecosystem functioning: mycorrhizal fungi contribute to primary production (van der Heijden & Horton 2009; Kennedy 2010), and saprotrophic fungi recycle biomass (Griffith & Roderick 2008; Lindahl & Boberg 2008). Ectomycorrhizal agarics are mutualistic and provide nitrogen, phosphorus and water to plants and in exchange receive carbon, whereas saprotrophic agarics acquire their nutrients from enzymatic decomposition of organic substances (Moore et al. 2011).

Fungi show a fascinating diversity in life history strategies as well as morphology (e.g. Spooner & Roberts 2005). The most conspicuous morphological diversity is the enormous variability in size, colour and shape of the fruit bodies, which rivals

* *Corresponding author.*
E-mail address: claus.baessler@npv-bw.bayern.de (C. Bässler).
http://dx.doi.org/10.1016/j.funeco.2014.06.005
1754-5048/

the size, colour and shape of flowers in angiosperms (Hibbett & Binder 2002, see also Fig 1). Although there is no hard evidence that this morphological variability in fruit bodies is the result of an evolutionary adaptive response (see Gould & Lewontin 1979), examples suggest some selective pressure on fruit bodies (e.g. from suilloid over secotioid to hypogeous forms as an adaption to reducing desiccation; Bruns et al. 1989). However, compared to our understanding of flower or seed size in angiosperms (e.g. Leishman 2001; Westoby et al. 1992), we have only a limited understanding of possible correlates of fruit body size with other life history traits in higher fungi.

A species with a large fruit body is expected to produce more spores than species with small fruit bodies (cf. Fischer & Money 2010). If the number of spores is critical for successful reproduction, species with large spores should also have a large fruit body (Kauserud et al. 2008). However, large fruit bodies may also have disadvantages, such as attracting fungivores, although some fungivores, e.g. small mammals, act also as dispersal vectors, which is an advantage (cf. Johnson 1996; Luoma et al. 2003). Furthermore, and similar to seed size in higher plants, fungal spore size may also be linked to nutrient reserves and a higher survival success (for a compilation of the adaptive value of spore traits of fungi, see Table S1). However, in contrast to seeds of plants (Fenner 2000), fungal spores are tiny and are produced in large numbers (Buller 1909; Kramer 1982). This suggests that dispersal is a key for the reproductive success of fungi (Norros et al. 2012).

The size and number of fruit bodies produced determine the reproductive investment of a fungus individual and should depend on resource availability. Resource availability for saprotrophic fungi is variable, whereas the resource supplied to mutualistic fungi by their host is more reliable (Corrêa et al. 2011). Therefore, we expect saprotrophic agarics to produce fruit bodies on average smaller than those of mutualistic agarics. To test this hypothesis, we compiled data on fruit body size of species occurring in Northern and Central Europe. We used phylogenetically informed comparative analyses to test for differences in fruit body size and some other reproductive traits related to spores between saprotrophic and mutualistic agarics as well as trade-offs that might constrain fruit body size, and most importantly fruit body production.

Materials and methods

Fungal data

Data on the size of the fruit bodies as well as spore characteristics are available in the literature. However, information on the number of fruit bodies produced by a species is not available. Therefore, we used literature data complemented by field data for the present analyses.

1. From the literature, we compiled a data bank of fruit body and spore data (see below) of 592 saprotrophic and ectomycorrhizal (mutualistic) terricolous Agaricomycetes (Agaricales, Russulales and Boletales) across 91 genera that have the common agaricoid architecture of a fruit body with a central stem, cap and gills (see also Fig 1). The taxa were randomly selected on the basis of page numbers in the

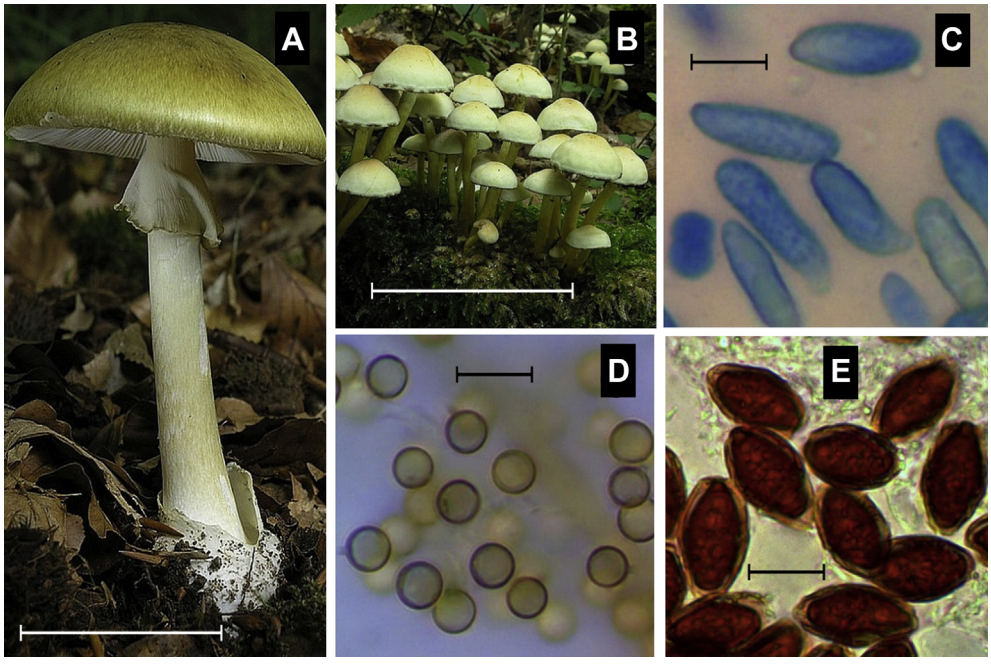

Fig 1 – (A) A tall and large fruit body of the ectomycorrhizal *Amanita phalloides* contrasts with (B) numerous, fasciculate and small fruit bodies of the saprotrophic *Hypholoma fasciculare*. The images (C–E) give an impression of the variability of basidiospores: (C) oblong, finely ornamented and large spores of *Ramaria longispora*, (D) globose, smooth, hyaline, thin-walled and small spores of *Lycoperdon marginatum* and (E) amygdaloid, melanised, medium-sized, thick-walled spores with germ pores of *Coprinopsis laanii* typical for this genus. In (A) and (B) bars are 10 cm, and in (C)–(E) 10 μm.

Funga Nordica (Knudsen & Vesterholt 2012) to represent approximately the proportional number of species within genera and sections of the species described in this source. We excluded *Hygrocybe* and grassland *Entoloma* because the exact trophic lifestyle of these species is not clear (Seitzman et al. 2011; Halbwachs et al. 2013; Tello et al. 2013).

2. We complemented this data set with data on fruit body production collected in the Bavarian Forest National Park in south-eastern Germany. The sampled area is covered by a low mountainous spruce (*Picea abies*) forest with boreal to alpine conditions and mean annual temperatures of 5.8–3.5 °C (Bässler 2004). Furthermore, this region is characterised by acidic soils (Bässler et al. 2010). We sampled agarics on 48 plots (plot size 200 m^2). Between 2009 and 2011, fruit body production was recorded weekly between June and November. During these field studies, 259 species were recorded. For these species, we also extracted fruit body and spore data from the *Funga Nordica* (see below). Only 3 of the 259 recorded species (~1 %) were not listed in the *Funga Nordica*; 60 % of the species were also included in our selection of species as described above. The total species list, therefore, consisted of 690 species (Table S2).

Fruit body size of all selected species was estimated using the squared cap diameter as a proxy for the fruit body biomass (Tóth & Feest 2007). From this source spore length and spore width (μm) were also extracted. The distribution of spore measurements within species is often skewed. However, Knudsen & Vesterholt (2012) ignored exceptionally small and large values and truncated the ranges. The numbers given refer to the interval where 90 % of the spores occur; therefore, the mean of the minimum and maximum is a reliable measure for our cross-species analysis, and the midpoint (= mean) was used for all further analyses. For the species recorded in the the Bavarian Forest, the number of all fruit bodies across the three sampled years was summed and that value divided by the number of plots on which the species occurred to get a relative measure of fruit body production. To get a robust measure, only species that occurred on at least four plots was used.

Across species, the distribution of the mean spore length and width is skewed (Fig S1). Therefore, both measures were $\log_{10}$-transformed for subsequent statistical analyses. Since these transformed measures are not independent from each other (Fig S2), both variables were subjected to a principal component analysis (PCA) on the covariance matrix of $\log_{10}$-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 PC2 indicate more elongated spores. Additionally spore volume was calculated from mean spore length and spore diameter, assuming an ellipsoid spore shape (cf. Kauserud et al. 2011), and a measure of spore shape was calculated as the ratio between spore length and spore diameter (Kauserud et al. 2011; Nordén et al. 2013) to enable a comparison with other studies (see Fig S1; for the complete species list and scoring of traits, see Table S2). Finally, our species data sets were divided into mycorrhizal (mutualistic) (literature data set 274 species; field data set: 159 species) and saprotrophic species (literature data set: 313 species; field data set: 100 species) according to Rinaldi et al. (2008).

Statistical methods

In comparative analyses of traits with a phylogenetic signal, the phylogeny has to be considered. Estimating this signal requires a phylogenetic tree that captures, at least approximately, the phylogenetic relationship between the analysed taxa. An approximate phylogenetic tree for the fungi was estimated in three steps. First, for all 690 species, a tree was constructed using published DNA-based trees (Moncalvo et al. 2002; Vellinga 2003; Garnica et al. 2005; Binder & Hibbett 2006; Matheny et al. 2006; Miller et al. 2006; Garnica et al. 2007; Saar et al. 2009; Vellinga 2010). The resulting tree (Table S3) had altogether 185 internal nodes and, therefore, 62 multifurcations (~34 %). Second, the approximate branch length was estimated by calibrating 10 nodes of the tree using relative ages of selected clades, based on a relaxed molecular clock analysis of a data set containing genes encoding two RNA polymerase II subunits (RPB 1 and RPB 2) and large and small subunits of nuclear ribosomal RNA (Hibbett & Matheny 2009); for a list of nodes and the relative ages, see Tables S4 and S5; for the nodes indicated on the tree, see Fig S3. Subsequently, we used the function *bladj* available in the program *phylocom* (Webb et al. 2008), which sets branch lengths by placing nodes without dates evenly between dated nodes. Third, a recent method was used to resolve nodes with models of diversification using published scripts (Kuhn et al. 2011) and the software *BEAST* (Drummond et al. 2012). This method provides a distribution of tree topologies and branch length. The distribution of trees and branch length was summarised using the software *TreeAnnotator* (Drummond et al. 2012) with default settings (target tree type: maximum clade credibility tree using the median for the relative age of the node). This tree was used as a master tree for estimating and testing the phylogenetic signal (Tables S6 and S7, Fig S4). A random sample of 100 trees from the distribution of trees was used to estimate the variability of the phylogenetic signal across the distribution of trees.

To test whether the variables showed a phylogenetic signal, Pagel's λ (Pagel 1999) and K-statistics were used (Blomberg et al. 2003); see also Muenkemueller et al. (2012). Significance was estimated by using 999 randomisations. To test whether the binary variable characterising whether a species belongs to the saprotroph or mutualist guild, the function *phylo.d* was used in the add-on package *caper* in R (Fritz & Purvis 2010). All four variables showed a clear phylogenetic signal (Table S7, Fig 2), and we had to use phylogenetically informed statistics for the subsequent analyses. Generalised linear models were used to test for differences in fruit body size; differences in spore volume and spore shape between saprotrophic and mutualistic species were analysed using a correlation structure derived from the Brownian motion model but in which the off-diagonal elements were multiplied by λ (Pagel 1999). The λ reported in Table S7 was used for the various variables. A random sample of 100 trees was used to estimate the variability of the difference between the two guilds.

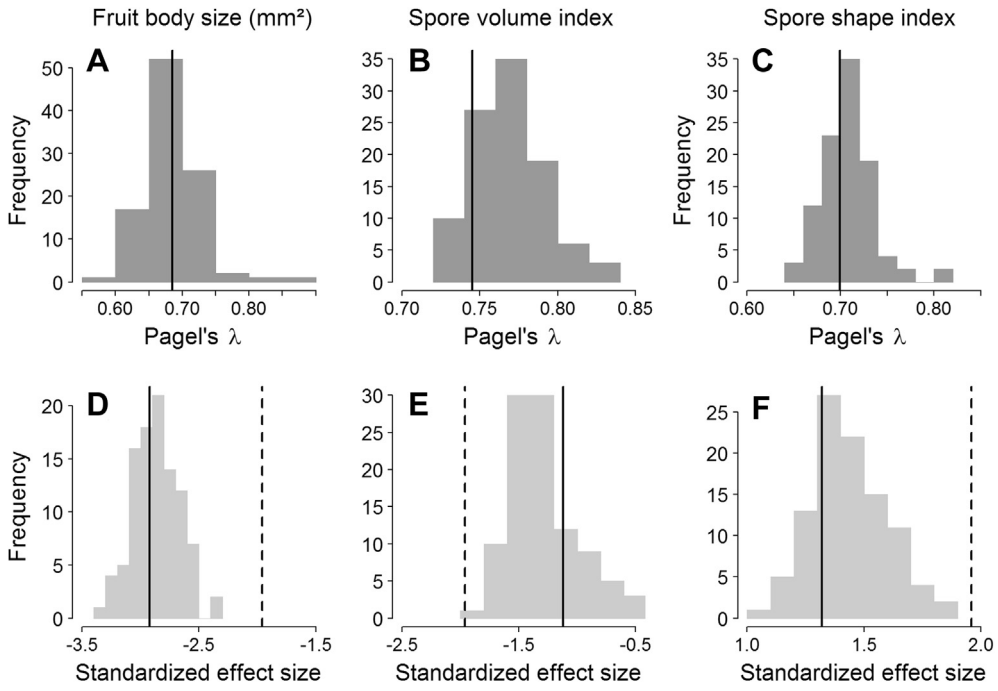

Fig 2 – (A–C) Distribution of Pagel's λ across 100 trees randomly sampled from the posterior distribution of resolved trees across all species. Note that for all three traits, Pagel's λ is probably between 0.6 and 0.8. Solid vertical lines indicate Pagel's λ from the master tree. (D–F) Standardised effect sizes (estimated divided by standard error, see Table 1) of the difference between mutualistic and saprotrophic fungi for fruit body size, spore size and spore shape. A negative effect size indicates that, e.g. fruit body size in saprotrophs is smaller than in mutualists. Values < -1.96 and > 1.96 indicate significant effect size. The 1.96 level of significance is indicated by the dashed line. Vertical solid lines indicate the standardised effects size from the generalised least-square models based on the master tree (see also Table 1).

Phylogenetically informed analysis was also used to test for correlations between variables.

Results

There were clear differences in fruit body size between saprotrophic and mutualistic agaric fungi, but no differences in spore size and spore shape (Table 1): mutualists had larger fruit bodies (Figs 2 and S4). The fruit body size of saprotrophs was significantly and negatively correlated with the number of fruit bodies produced: saprotrophic species with many fruit bodies on a plot produced small fruit bodies. Across both guilds, spore size showed a weak, but nevertheless significant positive correlation with fruit body size; the model revealed no difference between the slopes of the plots of the two guilds (Table 1, Fig 3). There was a significant relationship between fruit body size and the spore shape index only for saprotrophs, which indicated that large fruit bodies in this guild produced more spherical (globose) spores; the slopes of the plots of the two guilds did not differ (Fig 3).

Table 1 – Generalised least-square models using Pagel's correlation structure to test for differences in fruit body size, spore size and spore shape between mutualistic and saprotrophic fungi (guilds). For differences, mutualistic fungi are the reference group. Effect sizes (estimate divided by standard error); Fig 2 vertical lines in plots (D–F) that allow a comparison of the effect strength across models are given. For the two spore traits, fruit body size was included as a covariate (see Fig 3).

	Guild reference: mutualists	Fruit body size	R^2
Fruit body size	−2.92**		0.13***
Spore volume index	−1.12	2.38*	0.01**
Spore shape index	1.32	−1.35	0.07***

*<0.05, **<0.01, ***<0.001.

Discussion

Using a phylogenetically informed cross-species approach, we found that saprotrophic and ectomycorrhizal (mutualistic) agarics differ in fruit body size but not in spore characteristics. Most importantly, our comparisons demonstrated that mutualistic agarics produce on average larger fruit bodies than saprotrophic agarics. Such a phylogenetically informed analysis is the first step in showing that the variation of a trait across species is shaped by natural selection, of course within the context of the whole organism considering, for example, correlated responses or trade-offs (Gould & Lewontin 1979;

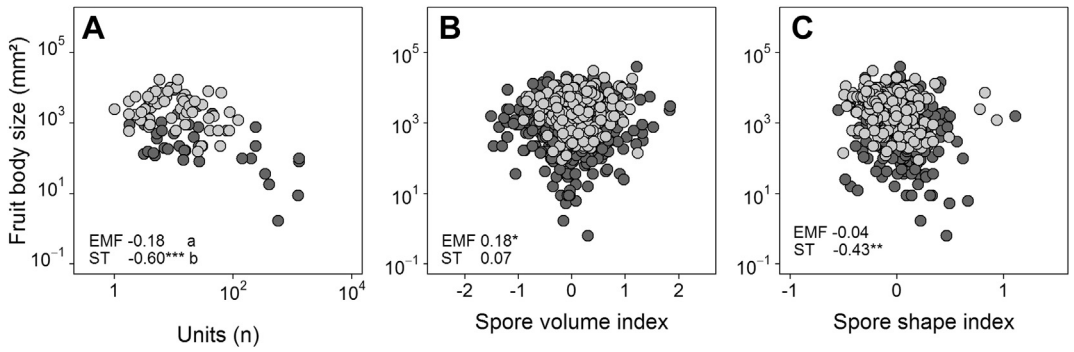

Fig 3 – (A) Relationship between fruit body size and number of units produced by each species across plots investigated in the Bavarian Forest, Germany. Note the negative relationship for saprotrophs (dark grey), which statistically differed from that of the mutualists (light grey), as indicated by two different letters. Within the plot, we give the raw slope from a generalised least-square model using Pagel's correlation structure to control for phylogeny. (B, C) Relationships between fruit body size and spore size as well as spore shape for mutualistic (light grey) and saprotrophic fungi (dark grey). Again the slopes are from a generalised least-square model with Pagel's correlation structure. The slopes were calculated separately for each guild, and therefore significance tests differ from the tests reported in Table 1.

Mayr 1983). However, note that modular organisms like fungi have more options to adjust form and function of traits to environment-induced needs than animals, where the "blueprint" induces evolutionary constraints (cf. Reich 2001).

Larger agarics generally possess a larger hymenial surface and are, therefore, able to produce more spores (cf. Kramer 1982; Fischer & Money 2010). Note also that the spore size of the two guilds did not differ. This suggests that ectomycorrhizal fungi are able to produce on average more spores than saprotrophic fungi. On the other hand, there might be a trade-off between fruit body size and number of fruit bodies. However, signs of such a trade-off were only found for saprotrophs. Nevertheless, note that the data related to this trade-off originate from only one study area and should, therefore, be interpreted with care. Furthermore, we have no information on the average genet size of the species, which makes it impossible to draw any conclusions on the overall investment in reproduction. Finally, we are aware that our comparison of saprotrophic and mutualistic fungi ignores the saprotrophic capabilities retained in some ectomycorrhizal species (Koide et al. 2008; Baldrian 2009; Cullings & Courty 2009). In some taxa, e.g. in *Amanita*, these capabilities have been lost (Wolfe et al. 2012); in others, e.g. *Laccaria*, saprotrophic enzymes assist in mobilising nitrogen needed for trade with the host (Martin et al. 2007, 2008).

Although the adaptationist programme has been heavily criticised as resulting in storytelling, these stories are nevertheless a heuristic approach to understand more about a trait (Futuyma 2013). There are probably three main advantages of a large fruit body size: (1) spore numbers, (2) dispersal capabilities and (3) advantages that might be summarised under the term "longevity".

(1) A large fruit body can generally produce more spores than a small fruit body. This suggests that fungi with large fruit bodies are less dispersal limited, which can become a major factor in fungal diversity (Peay et al. 2010). Furthermore, if a high amount of spores released is critical in the lifecycle of a species for successful survival, those that produce a large fruit body are able to optimize both the amount and size of the spores. However, note that we found no difference in spore size between the two groups of fungi.

(2) Spores of larger and, therefore, taller species will more easily leave the boundary layer of still air and disperse farther than spores of shorter species (Galante et al. 2011). Larger fruit bodies are generally also taller (Ingold 1946). Therefore, fungi with larger fruit bodies disperse over longer distances than fungi with small fruit bodies (cf. Buller 1909).

(3) The larger a fruit body is, the lower is the surface-to-volume ratio, and this might influence the degree of protection against pathogens or desiccation, which generally seems to be critical in the sporulation capacities of agarics (Buller 1909: 121, 123; Clémençon 1997: 598). Large fruit bodies are able to buffer temporal dryness (Buller 1909: 24). However, this relationship could also reflect architectural (static) constraints. Having a large fleshy trama and a stipe might act as defence against species feeding on the fruit body, or enhance attraction of animal dispersal vectors (cf. Bunyard 2007). Large fruit bodies may also have disadvantages, e.g. in attracting fungivores that do not act as dispersal vectors and only feed on these fruit bodies. Furthermore, the number of spores released may also depend on the life span of the fruit body. Although comprehensive studies on the relationship between size and longevity of fruit bodies are lacking, some evidence indicates that large fruit bodies survive longer than smaller ones (e.g. Haard & Kramer 1970; Richardson 1970); therefore, because fruit bodies sporulate as long as they remain vital (Haard & Kramer 1970; McKnight 1990; Moore et al. 2008), large fruit bodies would be able to produce more spores.

The above arguments suggest that large fruit bodies are associated with some advantages for the reproductive output. However, across the agarics, fruit body size varies considerably, and we showed here that saprotrophic fungi have

consistently smaller fruit bodies, which calls for an adaptive explanation. A further indication that fruit body and even spore traits have an adaptive component comes from the fact that the assemblage of fungi recorded during the field work is a non-random sample from the species pool (see Figs S5, S6). The most obvious difference between these two guilds is the allocation of carbon. There is some evidence that for ectomycorrhizal fungi, carbon is available in excess rather than being insufficient, and these fungi, therefore, seem not to be carbon limited (Corrêa et al. 2011). Saprotrophic fungi, on the other hand, need to invest energy by producing enzymes to gain carbon from recalcitrant organic matter, an ability ectomycorrhizal fungi have to a large extent lost, as e.g. in *Amanita* (Nagendran et al. 2009; Wolfe et al. 2012). Clearly, carbon availability from organic matter is highly variable within the saprotrophic guild and depends strongly on the recalcitrant character of the resource (wood, litter, humus). Ectomycorrhizal fungi are supported by their host, which might compensate for environmental constraints (Lilleskov et al. 2002; Corrêa et al. 2011). Thus, if ectomycorrhizal fungi are not C limited, then the on-average larger fruit body size might be simply related to the C access provided by the host. In line with this hypothesis, no trade-off between fruit body size and fruit body production was found in the mutualistic guild. Small fruit bodies may have some further advantage when colonising patchy niches, as is the case for fungal litter decomposers. Species with small fruit bodies thereby have the option of a finer-grained response of the reproductive investment than species with large fruit bodies.

Overall, the phylogenetically informed analysis showed clear evidence that saprotrophic fungi have smaller fruit bodies than mutualistic fungi. We argue that this difference is related to resource availability. Ectomycorrhizal fungi receive carbon from their hosts, and without C limitation, evolution might favour large fruit bodies in these species. In contrast, in saprotrophic fungi, fruit body size might have responded to resource availability and size of resource patches. However, many pieces of information are lacking. Most importantly, our arguments rest on the notion that reproductive investment depends on degrees of freedom in resource allocation. Future studies need to quantify resource investment of genets. Nevertheless, easier options to further test our ideas are available. We note here only three possibilities. First, by improving the phylogenetic tree, we might reconstruct fruit body size and resource acquisition across the tree. This would allow testing whether the transition of a clade from a saprotrophic to a mutualistic lifestyle is associated with an increase in fruit body size across the tree. Second, analysing life history traits of co-occurring species across a steep environmental gradient would allow searching for the adaptive significance of fruit body size or other reproductive traits (see also Fig S5, Fig S6). Finally, in a cross-species approach, resource size and patchiness and fruit body size within the saprotrophic guild could be investigated.

Acknowledgements

The insightful reviews of two anonymous reviewers and Panu Halme improved the manuscript considerably. We are grateful to Reinhard Agerer and Franz Oberwinkler for helpful discussions and their critical appraisal of the manuscript. We thank Franz Oberwinkler also for data on spore traits of selected taxa that enabled us to validate our data set. We thank Andreas Gminder, Heinrich Holzer, Andreas Kunze, Lothar Krieglsteiner, Regina Siemianowski and Anna von Steen for help with field work, and Hartmut Schubert (www.harzpilzchen.oyla.de) and Georg Müller (www.pilzepilze.de) for providing the brilliant images used for the collage in Fig 1. We thank Karen A. Brune for linguistic revision of the manuscript.

Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.funeco.2014.06.005.

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