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LETTER

Symbiotic status alters fungal eco-evolutionary offspring trajectories

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Abstract

Despite host-fungal symbiotic interactions being ubiquitous in all ecosystems, understanding how symbiosis has shaped the ecology and evolution of fungal spores that are involved in dispersal and colonization of their hosts has been ignored in life-history studies. We assembled a spore morphology database covering over 26,000 species of free-living to symbiotic fungi of plants, insects and humans and found more than eight orders of variation in spore size. Evolutionary transitions in symbiotic status correlated with shifts in spore size, but the strength of this effect varied widely among phyla. Symbiotic status explained more variation than climatic variables in the current distribution of spore sizes of plant-associated fungi at a global scale while the dispersal potential of their spores is more restricted compared to free-living fungi. Our work advances life-history theory by highlighting how the interaction between symbiosis and offspring morphology shapes the reproductive and dispersal strategies among living forms.

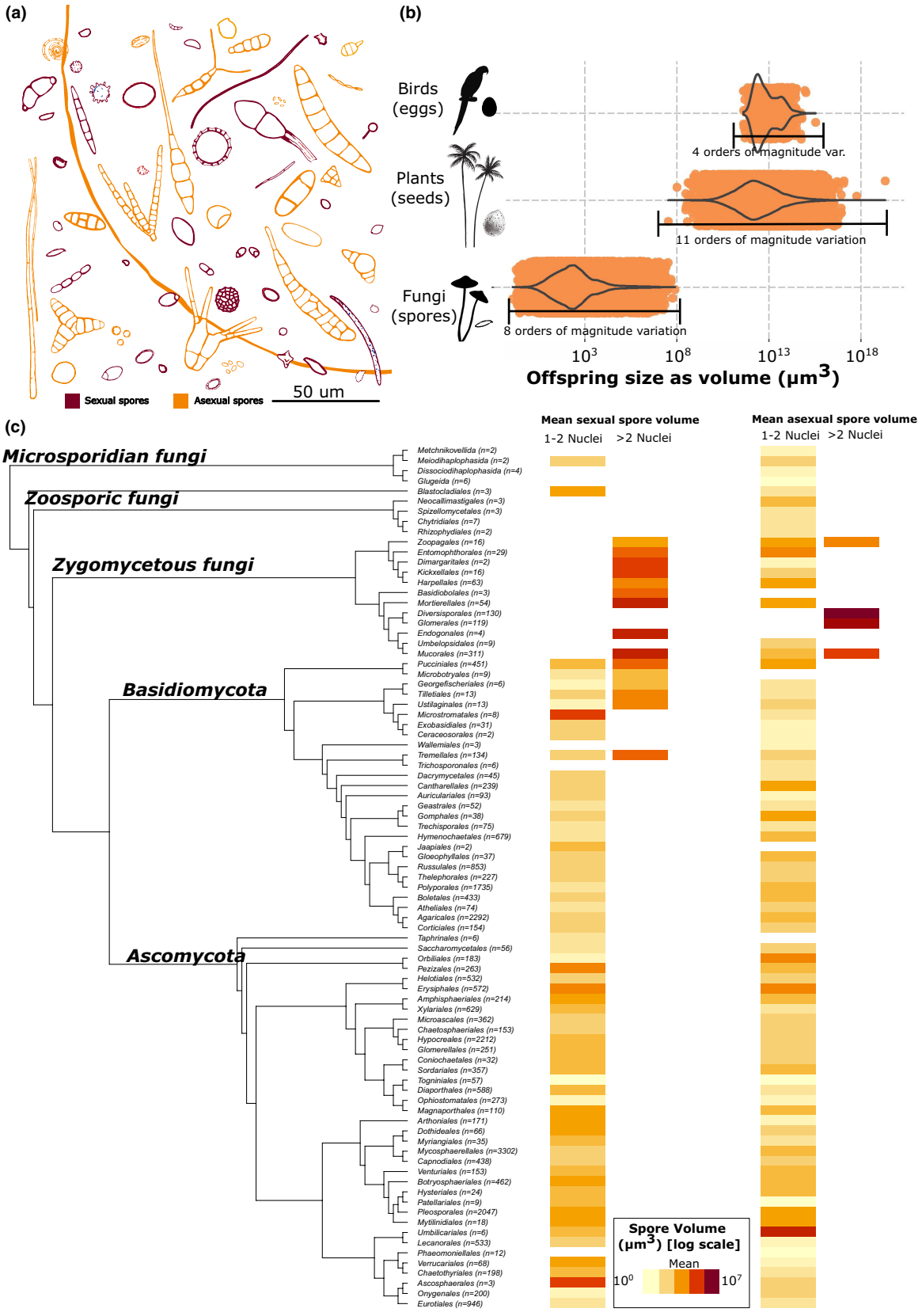
KEYWORDS
functional ecology, fungi, life-history, offspring size, symbiosis

INTRODUCTION

In life-history theory, the ecology and evolution of offspring size is linked to environmental factors that species encounter during reproduction, dispersal and early-colonization, as well as physiological constraints during their development (Stearns, 1992). By providing a common framework where disparate offspring structures such as plant seeds (Moles et al., 2005), animal ovules (Neuheimer et al., 2015), avian eggs (Stoddard et al., 2017) and mammal size at weaning (Falster et al., 2008) can be compared, life-history theory aims at discovering general principles behind the drivers shaping the ecology and evolution of species at earlier stages of their life cycle. According to life-history theory, alterations in the size of offspring structures of sessile organisms can influence their potential for both dispersal (moving to a new habitat) and colonization (establishing a new individual) (Falster et al., 2008; Kavanagh & Burns, 2014). The size of the offspring structure could impact how far it can disperse and its capacity to withstand environmental conditions during dispersal. Conversely, change in size alter the amount of resources that can be packed into offspring structures, resources which can facilitate germination and earlier stages of development that ultimately lead to successful colonization and the formation of a new functional individual.

However, most life forms that have been used to develop this knowledge are free-living macroorganisms, ignoring the large diversity of microbial forms. Conspicuously absent is the Kingdom Fungi, which, with 136,000 described species and an estimated diversity of 3–10 million species (Hawksworth & Lücking, 2017), is a large portion of the tree of life. This dearth represents a fundamental knowledge gap because, as we report here (Figure 1), variation in fungal offspring size (up to eight orders of magnitude) is as high or higher than that of macroorganisms whose comparative offspring studies (e.g. plant seeds and avian eggs) dominate the life-history theory (Figure 1). Here, we use fungal spores as offspring

FIGURE 1 Interspecific variation in spore size and symbiotic lifestyles across the fungal kingdom: (a) Illustration of the diversity of shapes and sizes among all fungal sexual and asexual spore types. (b) Interspecific spore size variation is more than eight orders of magnitude across the kingdom, ranging from the mitospores of *Phoma muscivora* of 9.0×10^{-2} μm^3 to multinucleate spores of the mycorrhizal fungus *Scutellospora scutata* of 7.8×10^7 μm^3. This variation is comparable to that of other offspring structures such as angiosperm seeds and bird eggs (to aid comparison, all offspring structures are presented on the same scale [μm^3]). (c) Phylogenetic tree with terminal branches representing orders (the number of species per order for which we collected spore data is given in parenthesis). The corresponding heatmap displays order averages (in logarithmic scale) of spore size as volume in yellow-to-red colour scale for sexual and asexual spores separating spores types based on the number of nuclei, which is a major distinction in spore types for fungi (see main text and supplementary material for a detailed explanation on descriptions of the biology of these distinct spores). Fungal spores (n = 26, 134 species), avian egg data (n = 1395 species) were obtained from[7], while seed data (n = 34,390 species) were obtained from the seed database of Kew Botanical Garden (http://data.kew.org/sid/?_ga=2.73581714.1287366807.1501084977-1309187973.1501084964).



structures (Figure 1b) because they represent reproductive output units produced by a mature mycelium (the 'parent' fungus) that function as dispersal propagules to colonize novel habitats that are usually distantly located from the parental fungus. Each spore has the potential to develop into a new mycelium, which is independent from the parental one in the new habitat. Spore traits, such as total size, are hypothesized to determine the

likelihood of colonization based on spore interactions with their environment during their release, movement, attachment/landing, dormancy and germination (Golan & Pringle, 2017; Halbwachs, 2015; Kivlin, 2020; Rockett & Kramer, 1974). Thus, spores are functionally analogous to dispersal offspring propagules of other sessile modular organisms like plant seeds (Moles et al., 2005) or marine invertebrate eggs (Neuheimer et al., 2015).

We hypothesize that symbiotic status of fungal species may explain this large variation in spore size because of the contrasting conditions that spores encounter when germinating and colonizing dead organic matter versus living hosts. That is, most extant fungi can be placed along a symbiotic spectrum spanning from asymbiotic species whose spores start the colonization of organic matter substrates, to a variety of symbiotic interactions whose spores initiate the colonization (i.e. infection) in hosts in almost all major domains of life (Lutzoni et al., 2018; Naranjo-Ortiz & Gabaldon, 2019) (Figure 2; Figures S3 and S4). Furthermore, shifts between free-living to symbiotic life styles have been a major driver in trait evolution in the fungal kingdom (Lutzoni et al., 2018; Naranjo-Ortiz & Gabaldon, 2019) raising the question of how transitions in symbiotic status influence the ecology and evolution of spores. Here, we use a definition of symbiosis that is common in evolutionary biology: the intimate physical living together of distinct species (usually distantly related), whether mutualistic, parasitic, or commensal, including macrobe-microbe interactions, where the former is considered the 'host' and the latter the 'symbiont' (Chomicki et al., 2020).

Specifically, to understand the importance of symbiotic status in explaining differences in the size and function of spores across the fungal kingdom, we asked three questions. First, are transitions in symbiotic status correlated with shifts in spore size? To answer this question, we used linear phylogenetic regression to test whether the spore size of symbiotic groups (e.g. insect pathogens, plant pathogens, ectomycorrhizal) shift in size (i.e. increase or decrease) compared to asymbiotic fungi across all major fungal phyla. We then focused on plant-associated fungi in the Dikarya clade to test whether symbiotic groups of obligate lifestyles have larger offspring than symbiotic groups with facultative lifestyles. We focus on fungi associated to plants in this clade because plants are by far the host type with the largest diversification of symbiotic lifestyles (Lutzoni et al., 2018). In addition, this hypothesis has been repeatedly used to explain why the spores of some obligate plant pathogenic and mutualistic fungi are so large. This hypothesis posits that obligate symbionts may benefit from the greater resources present in large spores, since these resources represent the only means of surviving during dispersal and initial colonization (i.e. infection) of new hosts until resources can be exchanged with the host plant (Garrett, 1970; McLaughlin & Spatafora, 2014). Second, we asked whether spore size distribution across fungal communities at a global scale can be explained by climate variables, regardless of symbiotic status. We hypothesized that climate may be more important than symbiotic status in explaining spore size distributions given the worldwide distribution of fungi spanning diverse climatic zones. As both asymbiotic and plant-associated fungal species release and disperse their spores into the abiotic environment, climate may act as a key driver of spore size variation (Kendrick, 2017). In addition, based on predictions from life-history theory, we expect species with larger offspring sizes to be associated with limiting environmental regimes (Moles & Westoby, 2004). Third, we asked whether the dispersal potential of spores differs between asymbiotic and plant-associated fungi. Specifically, we tested whether species with smaller spores have a broader geographic distribution (i.e. higher extent of occurrence) and whether this relationship varies between asymbiotic and plant-associated fungi. One of the main ecological functions of offspring is dispersal and, for several fungal groups, it has been proposed that small offspring should travel farther than large offspring, increasing the dispersal potential of species (Norros et al., 2014). However, if plant-associated fungi require large spore sizes, they may have more-limited distributions than asymbiotic fungi.

MATERIALS AND METHODS

Assembly of spore database

Unlike macroorganisms such as plants and animals, no databases of offspring morphology for fungi exist. Therefore, to answer our questions, we created and populated a new database by text mining nearly 100,000 taxonomic descriptions deposited in Mycobank (Robert et al., 2013) (http://www.mycobank.org/; see Supplementary material for further details). In total, we collected information on spore width and length dimensions for >26,000 accepted species (based on taxonomy from the Catalogue of Life; https://www.catalogueoflife.org/), representing 20% of all described fungal species (Figure S1). This database includes spore-dimension data from both sexually and asexually produced spores across major fungal lineages at different stages of fungal life cycles. However, we restricted the analysis described below to sexual spore types described as 'ascospores' and 'basidiospores' (henceforth referred to as 'sexual spores') and asexual spore types described as 'conidia' and 'sporangiospores' (henceforth referred to as 'asexual spores') because they represent the most frequently occurring types of spores in our dataset and thus can be compared across several fungal lineages and symbiotic groups (Figure 1c; Figure S2). We also excluded spores of glomeromycete fungi for our main analyses because their extreme large size may bias the results (see Figure S2 and supplementary material for specific spore definitions and nomenclature used in the analysis; Kendrick, 2017). We

then calculated spore volume using width and length as a proxy for spore size following the formula for a prolate spheroid (Aguilar-Trigueros et al., 2019). We used volume as a proxy for size because it captures the 3D structure of fungal spores and, based on allometric theory, volume scales with other measurements of size, such as weight. Indeed, volume has been used in life-history research as a proxy for offspring size across several large clades (Stearns, 1992). Using this approach, we found that spore size across species varied by more than eight orders of magnitude (Figure 1b).

Assembly of symbiotic status data

We also assembled a symbiotic status database (by mining and crosschecking different functional databases) where fungal species were categorized as asymbiotic (i.e. saprotrophic species that have only been reported as free-living during their whole life cycle) or symbiotic with a wide diversity of host and types of interactions as follows: (1) Asymbiotic saprotrophs; (2) Insect pathogens; (3) Lichen fungi; (4) Plant endophytes; (5) Plant pathogenic necrotrophs; (6) Plant pathogenic biotrophs; (7) Ectomycorrhizal fungi; (8) Arbuscular Mycorrhizal fungi; (10) Human pathogens. For plant symbiotic fungi, we further classify the level of specialization as either facultative symbiosis (species that are reported to alternate between a free-living and symbiotic phase) or obligate symbiosis (species that have been exclusively reported as symbiotic to complete their life cycle) based on the biology of their respective symbiotic group (see supplementary material for data sources and details on the criteria used to define symbiotic groups).

Phylogenetic regression of shifts in spore size and evolutionary transitions in symbiotic groups

Because evolutionary history shapes how and where species are today, the role of this history can be examined by testing how traits shift across the tree of life. For fungal spores, recent reviews and anecdotal evidence suggest that spore size is expected to differ more widely in some fungal clades than others (Aguilar-Trigueros et al., 2019; Ingold, 2001). Thus, we used two phylogenies to test whether transitions in symbiotic status correlate with shifts in fungal spore size. The first phylogeny consists of 1644 fungal species whose genome has been fully sequenced as recently published in (Li et al., 2021). Focusing our analysis on these species allowed us to incorporate the most robust, species-level phylogenetic tree available to date for fungi (as this tree is based on whole genome data) that captures the entire kingdom (i.e. it is not specific to only a subset of fungal clades). However, because this tree only includes a limited number of species, we also used a taxonomy-based phylogeny consisting of 23,000 species from which we obtained taxonomic data from phylum-to-species level using the function *as.phylo* from ape package (Paradis & Schliep, 2018) (see further details in the supplementary material for the construction of this tree).

Independently for each phylum or fungal group (i.e. Ascomycota, Basidiomycota, zygomycetous fungi, zoosporic fungi and microsporidan fungi), we conducted phylogenetic linear regression models where the logarithm of spore volume was the response variable, symbiotic status (based on the 10 symbiotic guilds classified here) was the explanatory variable and either the genome-based phylogenetic tree from (Li et al., 2021) or the taxonomy derived cladogram was used to account for phylogenetic relatedness. These phylogenetic regressions were conducted on sexual spores of the Ascomycota and Basidiomycota (i.e. ascospores and basidiospores) and asexual spores of all phyla and fungal groups (as defined above, we only include asexual spores referred as 'conidia' or 'sporangiospores') separately as they represent two separate traits under different selection. These phylogenetic linear regression models were conducted using the function phylolm from the phylolm package (Ho et al., 2016).

We conducted additional phylogenetic regression models testing whether spore size is bigger for obligate symbionts compared to facultative symbionts for sexual spores of plant-associated fungi in the Ascomycota and Basidiomycota and asexual spores of the Ascomycota. As above, this phylogenetic regressions were performed the genome-based phylogenetic tree (Li et al., 2021) or the taxonomy-based cladogram.

Relative importance of symbiotic status against climate variables in explaining spore size variation across communities

To obtain climatic information, we first mapped the geographic distributions of fungal species observed in several large-scale, high-throughput DNA-sequencing studies of fungal communities from soil and plant samples covering an extensive breadth of biomes and occurring on all seven continents (Figure S5; see supplementary material section for details on how species annotations were performed). Then, we collected climatic data associated with the locations where those species were found, estimated mean values for each species, and compared the ability of those climate variables and each species' symbiotic status to explain variation in spore size.

For this analysis, we focused on species that in our database are reported to produce only one spore type because it is not possible to determine the spore type associated with environmental DNA sequences. We assessed the importance of fungal symbiotic status (i.e. whether

fungi are free-living saprotroph or plant-associated) in explaining interspecific variation in spore size relative to other drivers, including spore type (i.e. sexual and asexual) and climate across communities worldwide. Phylogenetic linear regression models were fit using the following predictors: spore type (categorical variable), climate (averages of mean annual temperature and precipitation, temperature and precipitation seasonality, maximum solar radiation and minimum water-vapour pressure calculated across locations in which each species was detected; as continuous variables) and symbiotic status (as a categorical variable—free-living or plant-associated). As before, we conducted this analysis using two phylogenetic regression (one using the genome-based phylogenetic tree from (Li et al., 2021) and the other one using the taxonomy-based tree).

Differences between saprotrophic and plant-associated fungi in the relationship between spore size and geographic spread

We assessed the role that fungal lifestyle plays in determining the relationship between geographic range and spore size. As with the previous analysis, we focused on species that in our database are reported to produce only one spore type because it is not possible to determine the spore type associated with environmental DNA sequences. To do this, we estimated species' geographic ranges from their mapped distributions in environmental DNA-sequencing studies. Specifically, geographic range for each species was estimated in two ways: (1) as the maximum distance in meters between samples, in which the species was detected using the ellipsoid method (Vincenty, 1975) calculated with the distVincentyEllipsoid function from the 'geosphere' package in R (Hijmans et al., 2019); and (2) as the range area in square meters using alpha-hull-derived measures (Edelsbrunner et al., 1983) incorporating all samples in which the species was detected using the getDynamicAlphaHull function from the 'rangeBuilder' package in R (Davis Rabosky et al., 2016). Each estimate of range size was then used as a response variable in linear models to estimate slopes representing the strength of the relationship between geographic range and spore volume for fungi with saprotrophic lifestyles (free-living) and those from plant-associated lifestyles (symbiotic). These models included random intercepts representing the taxonomic order (to account for non-independence among fungal species) and the primer set used to amplify fungal DNA (to account for biases among primer sets in their ability to detect fungal species). Because point-estimates can be sensitive to unbalanced sampling designs and, therefore, are unreliable, we used functions in the 'lme4' (Bates et al., 2015) and 'brms' (Bürkner, 2017) packages in R to fit Bayesian models and estimate posterior distributions of the slope parameters and calculated 95%-credible intervals from four MCMC chains (each 2000 iterations with a 1000-iteration burn-in) to assess differences among fungal lifestyles. To assess relationships within individual orders, separate linear mixed-effects models were also fitted for each combination of taxonomic order and fungal lifestyle for which a minimum of five species with spore volume and geographic extent were available.

All statistical analyses were performed using R version 4.0.1 (Team, 2020). Spore volume was log10-transformed prior to statistical analyses.

RESULTS

Strong differences in spore size among fungal clades

Spore size variation among sexual and asexual spores was strongly structured by species' evolutionary history (Figure 1c, Tables S1 and S2). For instance, the asexual spores from the glomeromycetes are the largest in the kingdom, from 1.5-to-4 orders of magnitude larger compared to other spores (either sexual or asexual) from other groups and this difference shows strong phylogenetic structure (Pagel's lambda ~0.7 depending on the comparison, see Table S1). These spores of glomeromycetous fungi, however, are unique among other fungi because they contain hundreds of nuclei (an unparalleled feature in the kingdom (Kokkoris et al., 2020)), which might partly explain their extremely large size (Aguilar-Trigueros et al., 2019). Further, we found that sexual spores of basidiomycetes are on average 6 μm^3 smaller than ascomycetes across the tree (Pagel's lambda = 0.8, see Table S2). While this pattern alone cannot determine the mechanisms behind this size difference, it is consistent with the hypothesis that sexual spores of basidiomycetes are smaller than those of the ascomycetes because the Basidiomycota, as a whole, evolved a spore launching mechanism ('the surface tension catapult') that depends on spore size. In contrast, the launching mechanism of ascomycetes does not (Ingold, 2001; Roper & Seminara, 2019). This potential mechanism suggests that the size of the spore is dependent on the anatomy and morphology of the reproductive structure of the parental fungus. Such parent-to-offspring regulation has also been observed in other taxa, such as placental mammals, for whom size at birth depends on the anatomical constraints of the reproductive structure where the offspring develops (Stearns, 1992).

Correlation between transitions in symbiotic status and shifts in spore size vary among fungal clades

We found support for our hypothesis that evolutionary transitions in symbiotic status correlate with shifts

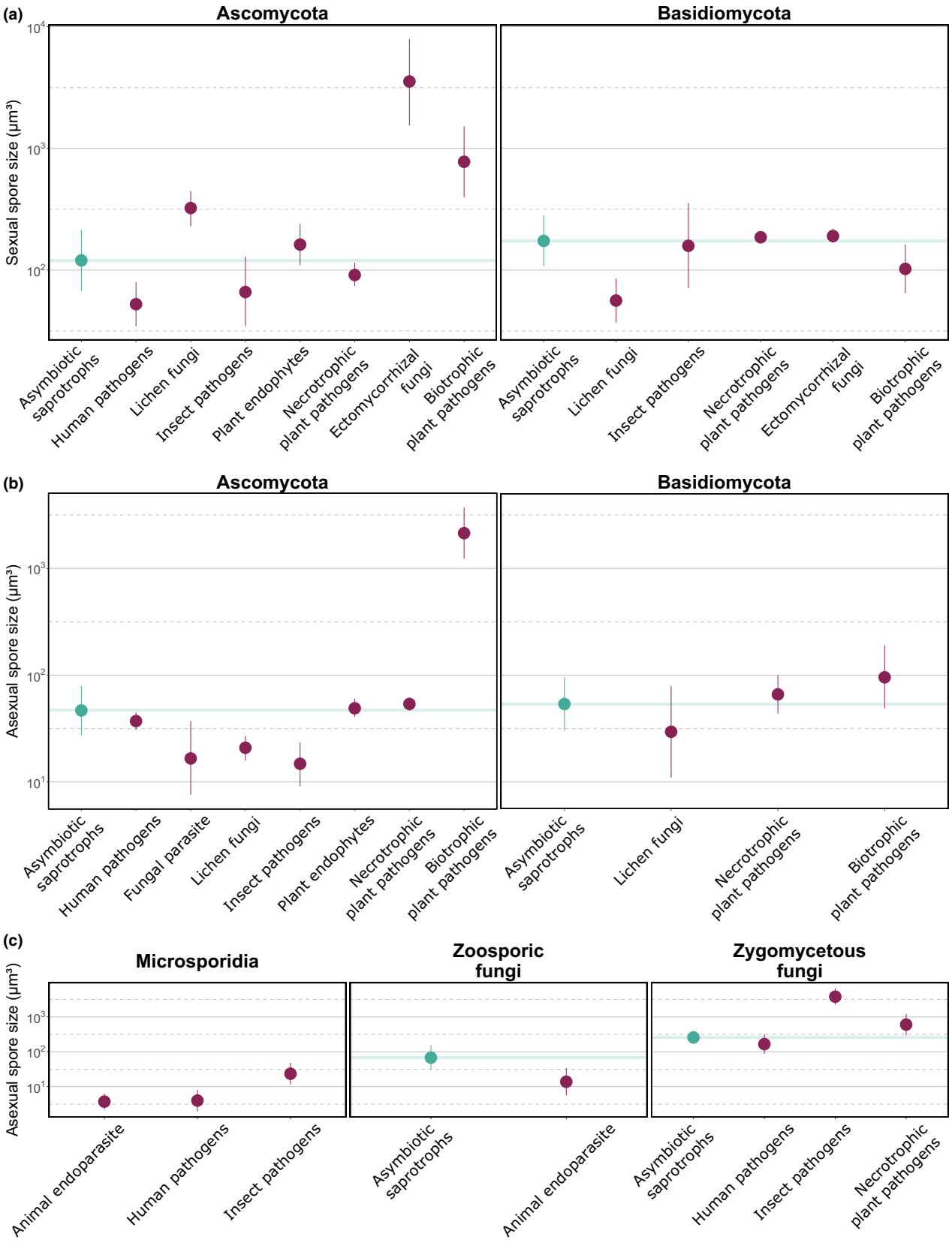


FIGURE 2 Shifts in size of sexual and asexual spores between asymbiotic fungi (blue points) and symbiotic groups (red points) across Dikarya (a, b) and non-Dikarya fungi (c). Point ranges show the predicted mean values (points) and associated standard errors (ranges) for each symbiotic group based on phylogenetic linear regression models using a taxonomy-based phylogeny. The horizontal blue lines are added to help comparison of asymbiotic and symbiotic fungi (except for Microsporidan fungi that have not recorded asymbiotic species). Similar results were obtained in models using a genome-based phylogeny (see Figure S2).

in the size of both sexual and asexual spores (Tables S3 and S4; Figure 2; Figure S3). However, the direction and strength of this correlation highly depended on the symbiotic group, spore type and phylum considered. We found that shifts in sexual spore size during transitions from saprotrophic to symbiotic groups were stronger in the Ascomycota compared to the Basidiomycota, specifically, we found shifts to larger spore sizes among insect pathogens, ectomycorrhizal, lichen and mildew fungi in the Ascomycota (although statistical support for the last two groups was found on only one phylogenetic regression; see Table S3). For asexual spores, we also observed stronger shifts of size and symbiotic status among groups in the Ascomycota compared to the Basidiomyota, although shifts in asexual spore sizes were more heterogeneous: shifts to larger asexual spores were associated with biotrophic and necrotrophic plant pathogens, while shifts to smaller asexual spore sizes were associated with lichen and insect pathogenic fungi (Table S4). Finally, we also detected shifts towards larger asexual spore sizes among insect and necrotrophic pathogens of zygomycetous fungi (Table S4) and for insect pathogens in the Microsporidia.

Among plant-associated fungi, we found a global trend towards increased sexual spore size in fungi with more obligate symbioses in the Ascomycota only (i.e. we found no statistical support for this hypothesis with plant-associated groups in the Basidiomycota). For sexual spores, plant obligate symbionts in the Ascomycota were about 29 μm^3 larger than spores of facultative symbionts counterparts, while for asexual spores, obligate symbionts were up to 59 μm^3 larger than spores of facultative symbionts (all p-values <0.001; Figure S4; Table S5). A possible mechanism behind large spores being associated with these groups is that spore reserves or thickening of spore cell walls increase chances of survival when dispersing to a host, overwintering and/or overcoming initial host resistance (e.g. penetration of the hard cuticle or the epidermal tissue) (Kemen & Jones, 2012; Wang & Wang, 2017).

Our results are congruent with previous research reporting small differences in spore size across functional groups in Basidiomycota fungi, particularly when comparing the sexual spores of ectomycorrhizal and saprotrophic fungi suggesting than other reproductive traits, such as sporocarp size and shape, might be more functional (Bässler et al., 2014; Calhim et al., 2018; Halbwachs et al., 2017; Kauserud et al., 2008). As we show here, this small difference might be due to the already small size of sexual spores of basidiomycete fungi relative to ascomycete fungi, which prompts the hypothesis that for the Basidiomycota the demand for small spores for the launching platform leaves little room for differentiation during evolution of the symbiotic lifestyle. In the case of necrotrophic pathogens or plant endophytes, the overlap in spore sizes with asymbiotic fungi and their relative large variation in sizes (Figure 2; Figure S3) may reflect differences in the level of symbiotic specialization (Mengiste, 2012) that is not captured with the current classification. Plant pathologists have long speculated that larger spores may provide the necessary resources for highly host-specialized necrotrophs to overcome host defences and infect healthy host tissue, while such resources may be less important among less specialized necrotrophic pathogens that can only infect weakened plants (Garrett, 1970). We also found large variation in spore size across asymbiotic saprotrophic fungi (for any group or spore type; Figure 2; Figure S3). This variation suggest the existence of different niches filled by saprotrophic species, such as during decay of different substrates or in different successional stages (Purhonen et al., 2020). Finally, we also included in a separate analysis the peculiar case of fungi that cause disease in humans due to their importance. Most of these fungi are described as opportunistic (i.e. causing disease in immuno-compromised individuals (Kendrick, 2017)) and are commonly found growing as free-living in nature; these fungi are, thus, generally considered asymbiotic rather than symbiotic in the mycological literature (Moore et al., 2011). Our results, however, show that such fungi, despite their expected asymbiotic nature, have on average smaller sizes than other asymbiotic fungi (a pattern that holds across the phylogeny in some of our models, Tables S3 and S4, Figure 2). While it is not possible to pinpoint mechanisms, we hypothesize that smaller spores for these fungi may enhance the likelihood to be passively inhaled or ingested (Moore et al., 2011).

Relative importance of species' symbiotic status in explaining offspring size variation

Symbiotic status was also more important for explaining interspecific variation in spore size than climate variables associated with the distributions of fungal species (Table 1). After symbiotic status, mean annual temperature was the second most important variable explaining spore size variation across communities. This is congruent with previous research highlighting that in some species of mushroom-forming fungi, thicker spore walls have higher resistance to UV light exposure and freezing temperatures than species with smaller and lighter spores (Norros et al., 2015). Possibly, for symbiotic fungi, environmental microclimate plays a minor role as the host will buffer these variables (e.g. fungal symbionts of warm-blooded fungal symbionts will be buffered against changes in environmental temperature).

Relationship between offspring size and species' geographic distributions depends on symbiotic status

Finally, we tested the relationships between spore size and geographic distributions for asymbiotic and

TABLE 1 Relative importance of symbiotic lifestyle versus climatic variables in explaining interspecific spore size variation. The fit of two phylogenetic linear regression models with lifestyle and six climatic variables as explanatory factors is compared to the fit of models in which one of these predictors was removed (indicated in the respective row). The first model uses the phylogenetic tree based on whole genome sequences as provided in (Li et al., 2021), which includes 281 species from which we collected climatic data (referred to as the 'genome tree model'). The second model uses a taxonomy-based cladogram for species based on their taxonomy from kingdom to species level (referred to as the 'taxonomy tree model'), which includes 1137 species from which we collected climatic data. AIC, Akaike's Information Criterion; *d*AIC, delta AIC (difference between the AIC of each model and the one containing all terms). A *d*AIC > 10 indicates no support for dropping that term from the model because it results in a large decline in model fit; dAIC between 4 and 7 indicate considerably low support for dropping that term; and dAIC<2 indicates strong support for dropping that term as it improves model fit (Burnham & Anderson, 2002).

Phylogenetic regression model	Adjusted r^2	Loglike	AIC	dAIC	Phylogeny used
All variables	0.21	−336.72	699.43		Genome tree
	0.09	−1328.2	2684.39		Taxonomy tree
(−) Symbiotic lifestyle	0.18	−341.41	706.82	7.39	Genome tree
	0.07	−1333.42	2690.85	6.45	Taxonomy tree
(−) mean annual temperature	0.21	−337.97	699.94	0.51	Genome tree
	0.09	−1328.23	2682.45	−1.94	Taxonomy tree
(−) mean annual precipitation	0.21	−337.25	698.49	−0.94	Genome tree
	0.09	−1328.34	2682.68	−1.71	Taxonomy tree
(−) Temperature seasonality	0.22	−337.02	698.04	−1.39	Genome tree
	0.09	−1328.23	2682.47	−1.93	Taxonomy tree
(−) Precipitation seasonality	0.21	−337	698	−1.43	Genome tree
	0.09	−1329.66	2685.32	0.93	Taxonomy tree
(−) Maximum solar radiation	0.18	−341.29	706.59	7.15	Genome tree
	0.08	−1330.52	2687.05	2.66	Taxonomy tree
(−) Minimum vapour pressure	0.22	−336.72	697.43	−2	Genome tree
	0.09	−1328.25	2682.49	−1.9	Taxonomy tree

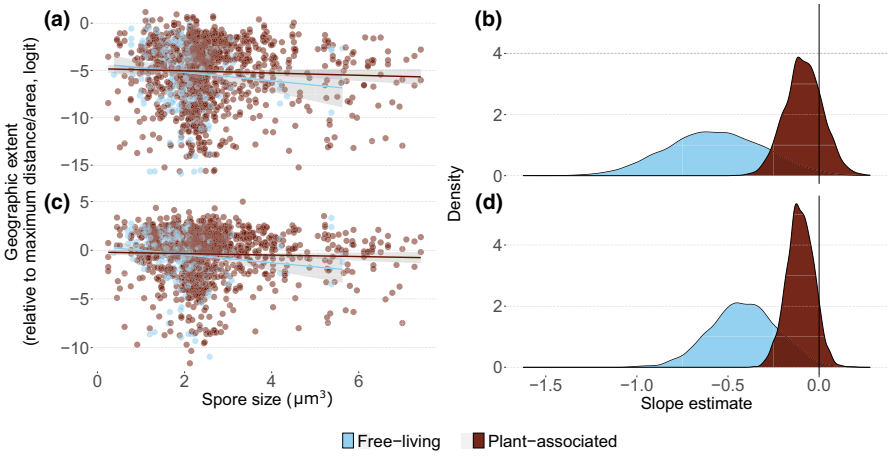


FIGURE 3 Asymbiotic fungal species exhibit a negative relationship between spore size and geographic distributions, while species plant-associated fungi do not. (a, c). Relationship between spore size and geographic distribution (based on polygon area [a] and the maximum distance between samples in which species were detected [c]) for asymbiotic fungal species and fungal species exhibiting varying degrees of host association to plants. Fungal species were detected in global surveys of environmental DNA from soil and plant material. (b, d) Bayesian models were fitted to estimate posterior distributions of the slope parameters representing the strength of the relationship between geographic extent and spore volume. The density plot represents the likelihood that a value associated with the slope estimate was present in the posterior distribution. These models included random intercepts representing the taxonomic order and spore type, as well as the primer set used to amplify fungal DNA (Tables S6–S8). Only species producing a single spore type were used in this analysis.

plant-associated fungal species, which we expect to be negative if smaller offspring size facilitates spread of propagules. Spore size was negatively correlated with the geographic range of free-living fungal species (95% credible interval for slope of maximum geographic distance: −0.71 to −0.11; 95% credible interval for slope of range area: −1.01 to −0.14; Figure 3) but not for symbiotic groups (95% credible intervals for slope of maximum distance: −0.23 to 0.01; 95% credible intervals for slope of range area: −0.25 to 0.09; Figure 3). In asymbiotic fungi, species with larger spores had a more-limited geographic range compared to species with smaller spores, which may move more easily to new environments. Conversely, geographic range was unrelated to spore size for symbiotic

species, for which host-related factors (including the geographic spread of the host itself) may offset any difference in dispersal due to spore size. For example, smaller spore sizes might actually reduce the chances of 'landing' on a suitable host because smaller spores remain more easily aloft (Norros et al., 2014). The role of other spore traits (such as appendage morphology or spore wall ornamentation) must be assessed to fully understand the dispersal of symbiotic fungi (Gareth Jones, 2006).

DISCUSSION

In this study, we uncover massive variation in spore size in the fungal kingdom whose ecology and evolution is partly explained by transitions in symbiotic status of the species. However, we also found that the direction of this effect (i.e. shifts to smaller or larger spore sizes in symbiotic fungi) and its importance varies widely among symbiotic groups and phyla. For plant-associated fungi in the Ascomycota, our results provide support to the hypothesis that as symbiosis transitions from facultative to obligate, large spore reserves become more important for their survival during dispersal to and assist colonization of the plant. The results emphasize the critical role of symbiotic relationships in driving the evolution of life-history traits, especially in Fungi and suggest two avenues for further research. First, determining the mechanisms behind correlations between shits in spore size along transition to symbiosis; and second, determining why in some symbiotic groups and clades, spore size does not change along symbiotic gradients. For example, shifts to smaller spore sizes in symbiotic groups could be explained by host transmission dynamics. In other symbiotic interactions, such as parasitic animals, it has been proposed that small-sized offspring propagules are produced to increase the chances of transmission when hosts are hard to locate (Poulin, 2011). Exploring the influence of host transmission dynamics on fungal reproductive ecology can reveal intricate life-history strategies in the Fungi beyond spore structures. Direct transmission between hosts, for instance, may reduce reliance on spore dispersal and instead utilize alternative structures like hyphal extensions (as observed in mycorrhizal fungi (Bielčik et al., 2019)) or yeast phenotypes (as it is commonly seen in most insect gut endosymbionts (Gibson & Hunter, 2010)). In addition, as host-symbiont specialization is a long-term evolutionary process (Chomicki et al., 2020), the age of symbiosis might be a predictor of reproductive trait changes (for both host and symbionts). Thus, we propose that the reliance of fungi in other ways of transmission other than spores might explain weaker correlation and symbiotic state we found in some clades. In those cases, variation in spore size might be driven by neutral processes such as drift (which we did not test). In order to test these hypothesis it would be necessary to include more species across different symbiotic lifestyles in phylogenetic studies (James et al., 2020) and the need to populate databases with fungal reproductive traits. Such data would allow tests of even the most fundamental tenets in life-history for the fungal branch of the tree of life, such as the existence of trade-offs in offspring output-offspring size or allometric scaling relationships between parent size and offspring size.

Finally, information on the diversity of dispersal and colonization strategies among asymbiotic and symbiotic fungi will be useful to forecast the impact of global change on ecosystem functions provided by fungi. For example, disease risk caused by fungal plant pathogens is forecasted to change with increasing global temperature (Chaloner et al., 2020). Such changes are likely due to direct effects on survival of spores during dispersal, and indirect effects of changing habitat quality (e.g. host susceptibility). Information on fungal dispersal strategies for symbiotic groups will refine forecasts of pathogen expansions and likelihood of pathogen spillover from natural ecosystems to croplands. Considering that fungi represent the main cause of crop yield losses and are a main threat to animal health (Fones et al., 2017), such refinements in forecasting are particularly relevant to maintain food security and ecosystem health.

In summary, expanding the realm of life-history analysis beyond plants and animals to other diverse and important clades such as fungi highlights symbiosis as a key biotic driver influencing the ecology and evolution of offspring-size variation. Life-history frameworks are biased towards free-living organisms (Falster et al., 2008; Stearns, 1992) with relatively limited inclusion of parasitic animals (Poulin, 2011). Yet, symbiosis is pervasive through the entire tree of life (including animals and plants) and, as we show here, it explains offspring variation among major clades in the fungal kingdom. Including symbiosis as a life-history parameter creates the need for new theoretical frameworks to determine, for instance, how much the host controls the offspring traits of the symbionts (as in fungi, and possibly bacteria and protists) and how much the symbionts control the offspring traits of their macroorganism hosts.

AUTHOR CONTRIBUTIONS

CAAT conceived the study together with FSK, WKC, JRP and MCR. WKC downloaded data from Mycobank. FSK developed the text mining algorithm. CAAT, JRP, CD and HZ mined the text data and cleaned spore data entries. CAAT digitized manually the spore size data not present in Mycobank, managed the spore database and assembled the fungal functional database. JRP managed and assembled climatic and geographic data. CAAT and JRP performed statistical analysis with input from WKC and FSK. CAAT wrote the first draft, and all authors contributed to the writing of the paper.

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CONFLICT OF INTEREST STATEMENT

The authors confirm that there are no competing interests.

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DATA AVAILABILITY STATEMENT

We confirm that all data and code used for this paper have been deposited in the database Fun^{Fun}: https://github.com/traitecoevo/fungaltrait as well as in a Zenodo (10.5281/zenodo.7953831) and GitHub repository (https://github.com/aguilart/Symbiotic-status-and-fungal-spore-size).

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