LETTER

Global analysis reveals an environmentally driven latitudinal pattern in mushroom size across fungal species

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Abstract

Although macroecology is a well-established field, much remains to be learned about the large-scale variation of fungal traits. We conducted a global analysis of mean fruit body size of 59 geographical regions worldwide, comprising 5340 fungal species exploring the response of fruit body size to latitude, resource availability and temperature. The results showed a hump-shaped relationship between mean fruit body size and distance to the equator. Areas with large fruit bodies were characterised by a high seasonality and an intermediate mean temperature. The responses of mutualistic species and saprotrophs were similar. These findings support the resource availability hypothesis, predicting large fruit bodies due to a seasonal resource surplus, and the thermoregulation hypothesis, according to which small fruit bodies offer a strategy to avoid heat and cold stress and therefore occur at temperature extremes. Fruit body size may thus be an adaptive trait driving the large-scale distribution of fungal species.

Keywords

Fungal traits, global biomes, latitudinal gradient, mean fruit body size, saprobic and ectomycorrhizal basidiomycetes.

INTRODUCTION

Functional traits determine the physiological performance of organisms, with consequences for individual fitness, vital rates and life-history evolution (Violle *et al.* 2007). Their comparison in species from different phylogenetic lineages provides insights into the general processes that determine biodiversity patterns (e.g. Swenson *et al.* 2012; Lamanna *et al.* 2014). The evolution and ecology of functional traits differ considerably between unitarian and modular organisms. Modular, often sessile organisms such as plants, have a much broader capability of responding to environmental constraints, either phenotypically or evolutionarily (Losos 2017). Nevertheless, the basic processes that influence modular and unitarian organisms follow the same principles. An example is the surface to volume ratio, which for all organisms has important consequences for their energy budgets and exchange of molecules. These shared features further imply clear trait-based trends along environmental gradients for both modular and unitarian organisms (Chown & Gaston 2010; Michaletz *et al.* 2015).

Mushroom-forming fungi (stipitate Agaricomycetes) are a large group of modular organisms characterised by a mycelium growing in substrates such as soil or dead wood. They include more than 20 000 species and are distributed across all climatic zones (Kirk *et al.* 2011). The majority of these fungal species have a saprotrophic or a mutualistic (ectomycorrhizal) lifestyle and are essential drivers of nutrient cycling and primary production (Dighton 2016). A characteristic trait of all mushroom-forming fungi is the production of above-ground fruit bodies ("mushrooms"), consisting of a cap and a stipe (Fig. 1). These structures are responsible for the production of spores, analogous to the plant seeds produced in fruits, but also for a number of other functions in ecosystems. For example mushrooms are the basis of complex food webs (Worthen 1988). The fruit body size of fungi varies tremendously across species, ranging from, e.g. *Cryptomarasmius sphaerodermus*, with a maximum cap diameter of 0.7 mm, to *Macrocybe titans*, with a cap diameter up to 1 m (Fig. 1). Both species belong to the saprotrophic guild.

In response to a given level of resource availability, an individual or species of mushroom-forming fungi may invest in either many small or a few large fruit bodies (Bässler *et al.* 2015), a trade-off that is also well known for seed formation in plants (Venable 1992). Species-specific differences in fruit body size reflect different ecological strategies (Halbwachs *et al.* 2016) and, despite phenotypic variability, the maximum size is evolutionarily conserved (Bässler *et al.* 2015; Varga *et al.* 2019). Spores released from larger fruit bodies more easily leave the boundary layer of still air and therefore disperse farther than spores of smaller fruit bodies (e.g. Dressaire *et al.* 2016). Large fruit bodies also have a generally longer life expectancy and sporulate over extended periods (Halbwachs *et al.* 2016). Conversely, among the advantages of a small fruit body are more rapid development, rapid

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Figure 1 Examples of mushrooms and their sizes. Top row (bars: 2 mm) (a) *Physalacria cryptomeriae* Berthier & Rogerson (image: Sue Rogerson **(cc)**), (b) *Galerina lubrica* A.H. Sm. (image: Oluna & Adolf Ceska **(cc)**), (c) *Mycena terena* Aronsen & Maas Geest. (image: Arne Aronsen **(cc)**), (d) *Cryptomarasmius corbariensis* (Roum.) T.S. Jenkinson & Desjardin (image: Nhu Nguyen **(cc)**). Centre row (bars: 10 cm) (e) *Lactarius controversus* Pers. (image: Puchatech K. **(cc)**), (f) *Catathelasma imperiale* (P. Karst.) Singer (image: North American Mycological Association **(cc)**). Bottom row (bars: 10 cm) (g) *Phlebopus marginatus* Watling & N.M. Greg. (image: Bob (ericos_bob) **(cc)**), (h) *Termitomyces titanicus* Pegler & Piearce (image: Blimeo **(cc)**). **(cc)** Creativecommons.org/licenses/by/3.0/deed.en.

sporulation and greater flexibility in adjusting reproductive biomass to ephemeral and fluctuating resources as well as climate conditions (Bässler *et al*. 2016).

The essential functions of the trait 'fruit body size' suggest that large-scale ecogeographical factors determining fruit body size should occur across the world's terrestrial ecosystems. Important drivers of fruit body size are (1) resource availability and (2) the thermal environment.

Fungi need a minimum size of mycelium to produce fruit bodies (Raudaskoski & Salonen 1984). For species producing large fruit bodies, this minimum size is larger compared to species producing small fruit bodies (Bässler *et al*. 2014). Thus, resource availability should influence the assembly of fungal species with respect to the fruit body size. In a study conducted at a local scale, we found a correlation between the mean fruit body size of mushroom assemblages and resource availability (Bässler *et al*. 2016). As described in our 'ecosystems biomass hypothesis' (Fig. 2b), if the fruit body size of assemblages correlates positively with ecosystem productivity, then assemblages of fungi in the tropics a region that contains the largest biomass stocks and the highest levels of productivity (Pan *et al*. 2013) should consist of many species with large fruit bodies. In addition to the overall level of available resources provided by a habitat, the seasonal distribution and

usability of those resources might also influence the mean fruit body size of assemblages. Two measures of seasonal resource availability are suggested by the existing literature. First, temperature and precipitation are strong factors controlling the quality and quantity of resources (Chapin III et al. 2011), with climate seasonality strongly related to the seasonal availability of resources (H-Acevedo & Currie 2003; Corlett & Lafrankie 1998; Williams & Middleton 2008; Tonkin *et al*. 2017). Second, Huston & Wolverton (2009) suggested a measure of seasonal resource surplus termed ecologically and evolutionarily relevant net primary production (eNPP), which represents the availability of resources during the period of an organism's growth and reproduction (i.e. the net primary productivity averaged over the growing season). If the seasonal surplus of resources exceeds the basic energetic and nutritional demands of fungi during the time that they grow and reproduce, then species living in such environments can evolve large fruit bodies. This would suggest that the fruit body size of an assemblage is positively related to climatic seasonality and eNPP, if other factors are not limiting. This relationship can be described by the 'seasonal resource surplus hypothesis' (Fig. 2b).

Fungi are ectothermic organisms and the temperature of the fruit body depends on its geometry. However, similar to the
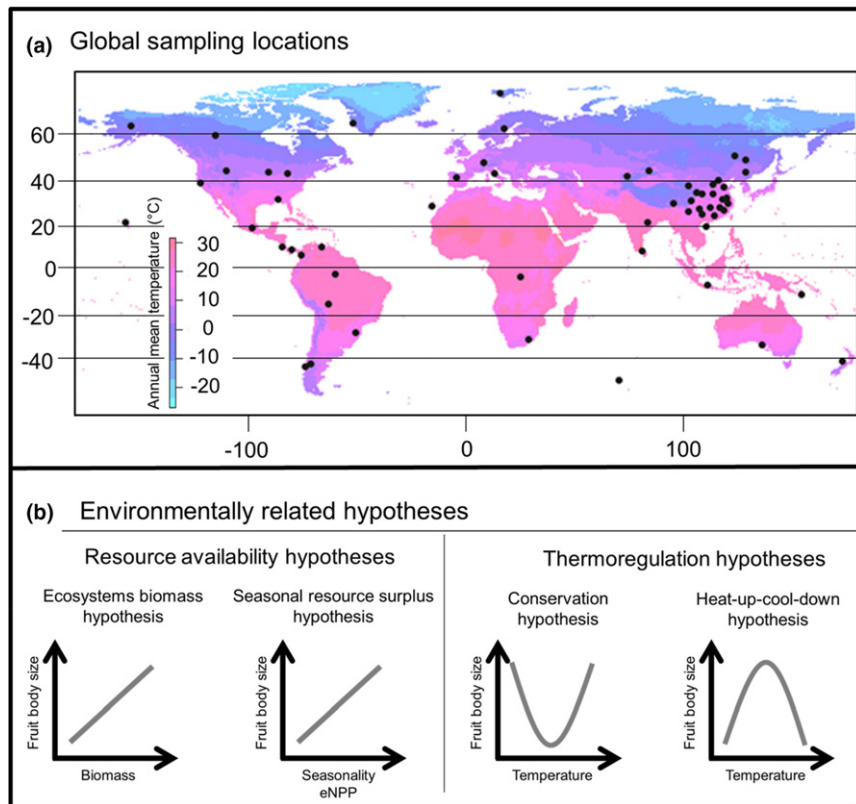
Figure 2 Sampling localities for the analysis of fruit body size and the hypotheses explaining fruit body size. (a) Global map showing the annual mean temperature. Black dots represent the centroid of each locality for which fruit body data were available (see the Methods section). (b) Hypotheses describing the relationship between fruit body size and both resource availability and temperature.

body size of ectothermic animals, such as insects, the relationship is not straightforward (Chown & Gaston 2010). Small fruit bodies have a higher surface-to-volume ratio and hence heat up and cool down more rapidly, a potential advantage in cold as well as hot environments. This should lead to a hump-shaped relationship between fruit body size and temperature, described by the 'heat-up-cool-down hypothesis' (Fig. 2b). However, fruit bodies with a lower surface-to-volume ratio have a higher thermal inertia that minimises both heat and cold stress (cold and heat retention). This scenario is accounted for by the 'conservation hypothesis' (Zamora-Camacho *et al.* 2014), which predicts a reversed hump-shaped pattern between fruit body size and temperature (Fig. 2b).

In this study, we compiled a global data set of fruit body size of *c.* 5300 taxa and then (1) explored the relationship between the mean fruit body size of fungal assemblages and the distance to the equator and (2) examined the hypotheses presented above with respect to resource availability (ecosystems biomass and seasonal resource surplus hypotheses) and temperature (heat-up-cool-down and conservation hypotheses).

MATERIALS AND METHODS

Fungal data

Only species with a fleshy stipitate fruit body (mushrooms) (Fig. 1) and only literature sources reporting the geographical distribution and fruit body size of the studied species were considered in this study. After a rigorous search of the internet, libraries, and textbooks, our study drew on 78 sources, consisting of fungas (fungal floras), monographs, field guides

and other published information (see Table SM1 for the complete list of sources and details of the search criteria and selection process). These sources cover a broad latitudinal and longitudinal range, and hence all major biomes (Fig. 2a, Fig, SM1). Some of the information contained in sources for the northern hemisphere within mid-latitudinal temperate systems (i.e. Western Europe and North America) was redundant. Thus, if one source was geographically and taxonomically duplicated by another that included a more comprehensive set of species, the latter was used to avoid pseudo-replication. Many of the included studies were vague about the exact sampling locations and referred only to larger geographical or administrative areas; nonetheless, most sources reported the occurrence of fungal species from geographically delimited units. In areas for which comprehensive fungal floras were not available, e.g. in parts of Southeast Asia, sources were combined. With this selection process, from the 78 sources species lists for 59 distinct geographical localities could be compiled for further analysis (Table SM2, Fig. SM1, Fig. 2a). The geographical boundaries of these localities were estimated based on information obtained from the selected sources and then defined using Google Maps or Google Earth. If the source only covered fungi from forests, a global forest map (https://www.globalforestwatch.org) was additionally used to adequately reflect the primary habitats of the collected mushrooms. Centroids were calculated based on the corner coordinates obtained from Google Maps (Fig. SM1). If a centroid fell on water, the value was corrected to the nearest point on land.

In local data sources, fruit body sizes were directly measured at the specific locality, and the values were, therefore,

more precise than those obtained from more general species accounts. For our database, we extracted the species names, updated using Index Fungorum (www.indexfungorum.org) and Mycobank (www.mycobank.org). In addition, for each record both the geographical data and the cap diameter, as a surrogate for mushroom size, were extracted. For species with several records, the cap diameter determined at the respective locality was used. Therefore, our study considered intraspecific variation and thereby presumably also local adaptation. The 6739 records compiled for this study represent 5340 species covering eight orders, 44 families, and 349 genera. Cap diameter (mm) is a reliable proxy for the dry weight (g) of a stipitate fruit body (e.g. Bässler *et al.* 2015). Since most of the sources provided information on cap size maxima only, the maximum size was used in our analyses, as it allowed the inclusion of all sources compiled for this study (see Fig. SM2 for details). In addition, the following information was assigned to each record: (1) nutritional mode, i.e. ectomycorrhizal (ECM) or saprotrophic (SAP), as reported in recent studies (e.g. Tedersoo *et al.* 2014), and (2) the geographical centroid and boundaries, based on the latitude and longitude of the respective geographical entity. With respect to nutritional mode, pure pathogens were not considered since they represented <1% of the records within our data set.

Environmental predictors

Distance to the equator (see also Tedersoo *et al.* 2014) was used to explore the spatial pattern of fruit body size and its relationship to specific environmental variables and thus to examine the four hypotheses (Fig. 2b). The predictor 'distance to the equator' was based on the latitudinal coordinates (degrees) of the centroids for each locality (see Fungal data). All environmental variables used to examine the hypotheses were matched to the included localities (represented as polygons, Fig. SM1) using the R-package 'raster' (Hijmans & van Etten 2012), with the mean of each variable calculated for each locality defined by a polygon. The ecosystems biomass hypothesis (Fig. 2b) was examined using the mean total tree biomass between 1950 and 2010 (in megatons per 1-degree grid cell), recorded in the database 'Global 1-Degree Maps of Forest Area, Carbon Stocks, and Biomass, 1950–2010' (Hengeveld *et al.* 2015). This measure was chosen since the clear majority of the fungal records derived from forest ecosystems. Note that in our data set total biomass correlated closely with aboveground biomass and forest carbon stock ($r > 0.99$, obtained from Hengeveld *et al.* 2015) and with net primary productivity ($r > 0.80$, obtained from Imhoff & Lahouari 2006). Thus, in our study only total biomass was used as an estimate of total resource availability. The seasonal resource surplus hypothesis (Fig. 2b) was examined using three independent variables: (1) temperature seasonality (BIO4, standard deviation *100; resolution 10´), as provided by WorldClim (Fick & Hijmans 2017), (2) precipitation seasonality (BIO15, CV = coefficient of variation, extracted from WorldClim) and (3) eNPP. To account for the fact that temperature seasonality correlates with annual mean temperature and is thus confounded by the direct (thermal) and indirect (e.g. productivity, Chapin III *et al.* 2011)

effects of temperature, the residuals from a simple regression of seasonality on mean temperature were used. Precipitation seasonality was included because seasonal resource surplus may also be driven by annual variations of precipitation (e.g. Williams & Middleton 2008). The eNPP was calculated by dividing the mean NPP (see above) by the mean growing degree days (GDD, obtained from New *et al.* 1999) for each locality. Calculation of the GDD provides a heuristic tool to measure heat accumulation and thus predict plant and animal growth as well as development rates (Cayton *et al.* 2015), based on the assumption that development will occur only if the temperature exceeds some minimum temperature T_{Base}:

$$GDD = [(T_{max} + T_{min})/2] - T_{Base},$$

where T_{max} and T_{min} are the daily maximum and minimum air temperature (McMaster & Wilhelm 1997). The annual GDD is the average number of GDDs that accumulate in a particular locality under normal climatic conditions. A temperature of 5 °C was used to compute monthly GDDs, with the resulting values then summed to estimate an annual GDD. Note that Huston & Wolverton (2009) calculated eNPP by dividing NPP by the length of the growing season which, however, resembles eNPP based on GDD ($r = 0.80$ and slope *c.* 1 based on a log-log regression using the data provided by Huston & Wolverton 2011). The relationship between fruit body size and temperature (heat-up-cool-down hypothesis and conservation hypothesis, Fig. 2B) was examined using the annual mean temperature (BIO1, °C). Thus, the main predictors used to examine our hypotheses were total biomass (log_{10}-transformed), temperature seasonality (residuals), precipitation seasonality, eNPP (log_{10}-transformed), and annual mean temperature. Since the environmental variables for two localities were incomplete, the hypotheses were examined based on 57 localities. The pairwise correlation among the environmental predictors was low ($|r| < 0.65$).

Statistical methods

Two types of response variables were modelled and two different predictor sets were used, for a total of four models. The first response variable was the mean of the log_{10}-transformed maximum cap diameter across species of each locality (Bässler *et al.* 2016). For simplicity, in the following this approach is referred to as 'assemblage-level', and the response variable the 'assemblage fruit body size'. The second response variable was the log_{10}-transformed maximum cap diameter of a given species in a given locality. This approach is referred to as the 'cross-species approach' and the response variable as the 'species fruit body size'. Based on both response variables, (1) the distance to the equator was used as a predictor to explore the spatial pattern of fruit body size and (2) the environmental variables were used to examine our hypotheses (Fig. 2b).

For the assemblage approach, only those localities with a minimum of five species were considered (51 out of 59 localities for the distance to equator analyses and 50 out of 59 localities for the environmental analyses). Due to the reduced number of localities, for this approach, all species were used and potential interactions between guild and other

independent variables were not considered. However, in the cross-species approach, the guild was included as a factor with two levels (ECM and SAP) and guild-specific effects as well as potential interactions between the guilds and other independent variables were considered. Since the number of available localities within the southern hemisphere was low, potential differences between the southern and northern hemispheres were not evaluated. Also, to take into account the possibility of a nonlinear relationship between the response variable and our independent variables, generalised additive models (GAM's, function 'gamm4', package 'gamm4', Wood 2017) within the software 'R' (R Core Team 2020) were fitted, with thin plate regression splines used for smoothing (Wood 2003).

Distance to the equator analyses
The assemblage comprising fruit body sizes across all species was fitted with a smooth, indicated by the 's(Distance_equator)' within the formulas, as a function of the distance to the equator. The predictor 'distance to the equator' allowed the pooling of localities from the northern and southern hemispheres. This model was formulated as follows:

Model 1: Mean_fruit_body_size ~ s(Distance_equator).

Next, the relationship of species fruit body size to the distance to the equator was explored (cross-species approach). As noted above, the guild of the species was included as a second independent variable and the estimate for each guild was fitted using the 'by'-argument to construct the smooth (Wood 2017). Possible differences in these estimates between guilds were considered by fitting an auxiliary model that included the interaction between distance to the equator and the guild. A significant interaction indicated that the latitudinal pattern in fruit body size differed between the two guilds. As species are not independent, prior to the formal analyses, the variance components across taxonomic levels (order, family and genus) were estimated for fruit body size using the function 'varcomp' (Venables & Ripley 2002) within the 'ape' package (Paradis 2012) . Since 'genus' was the component with the highest variance for fruit body size across taxonomic levels (Fig. SM3), it was considered as a random effect within the species models to account for phylogenetic autocorrelation. Moreover, as the same species were recorded in several localities, species names were also considered as a random effect nested within genus. Fruit body size may also differ between regions due to the biogeographical affiliations of species (Tedersoo *et al.* 2014). Therefore, as in the case of taxonomy, variance components were calculated. Although the variance components of region and localities were small (Fig. SM3), locality was considered as an additional random effect to account for the repeated measurement of species within localities. The model was formulated as follows:

Model 2: Species_fruit_body_size ~ Guild + s(Distance_equator, by = Guild), random ~ (1|Genus/Species) + (1|Locality)

Adding other taxonomic levels (order, family) to the nested term did not yield different results (Fig. SR1). Furthermore,

the spatial autocorrelations of the residuals of our models were weak but robust inferences were obtained by accounting for spatial autocorrelations in the models (Fig. SR2).

Environmental analysis

Following the rationale described for the distance to the equator analyses, the assemblage fruit body size across all species was fitted with a smooth as a function of the environmental predictors. The model was formulated as follows:

Model 3: Mean_fruit_body_size ~ s(Biomass) + s(Temperature_seasonality) + s(Precipitation_seasonality) + s(eNPP) + s(Temperature)

As outlined above for the distance to the equator analyses, for the cross-species approach guild was included as a factor with two levels (ECM and SAP) and guild-specific effects were estimated. After a visual assessment of the raw smooths and applying the 'gam.check' function provided within the 'mgcv' package (Wood 2017), we decided to limit the smooth splines to 5 knots. The model was formulated as follows:

Model 4: Species_fruit_body_size ~ Guild + s(Biomass, by = Guild, k = 5) + s(Temperature_seasonality , by = Guild, k = 5) + s(Precipitation_seasonality , by = Guild, k = 5) + s(eNPP , by = Guild, k = 5) + s(Temperature, by = Guild, k = 5), random ~ (1|Genus/Species) + (1|Locality).

As demonstrated in the distance to the equator analyses, alternative models considering additional taxonomic levels and spatial autocorrelation did not yield different results (Fig. SR1, SR3). Finally, it should be noted that the validity of the predictors related to our main hypotheses might be offset by other factors, especially mean precipitation and soil-related variables (Tedersoo *et al.* 2014). However, mean precipitation correlated closely with mean temperature ($r = 0.73$) and was therefore not considered to avoid distortion of the models due to closely correlated predictors (Dormann *et al.* 2013). A consideration of soil-related variables did not change the inferences (Fig. SR4).

RESULTS

Fruit body size and distance to the equator

The relationship between fruit body size and distance to the equator was hump-shaped at the assemblage level (Model 1, Table 1, Fig. 3). The same pattern was found for the two guilds at the cross-species level although the shape of the relationship differed slightly between them (Model 2, Table 1, Fig. 3). The peak in fruit body size occurred at a distance to the equator of 30–40° (3300–4400 km north or south of the equator). This finding was supported by a cross-species model considering all species (see also Table SR1, Fig. SR5). Fruit body size of ECM species was, on average, larger than those of SAP species (Fig. 3). A graphical assessment of the relationship between species fruit body size and distance to the equator for the hemispheres, selected genera and regions generally supported the overall finding (Fig. SR6–8).

Table 1 Distance to the equator models

| | Guild: ECM | Distance equator | | | |
	t-value	d.f.	*F*	Adj. *R²*
Assemblage level	All		3.53	**8.49*****	0.37
Cross-species level	ECM	−8.98***	3.01	**5.28****	0.22
	SAP		3.26	**4.02****	

Results of the generalised additive models for fruit body size vs. distance to the equator at the assemblage (Statistical methods, Model 1) and cross-species (Statistical methods, Model 2) levels. For the cross-species level, the guild (ECM = ectomycorrhizal and SAP = saprotrophic) was also included. The reference group used to simultaneously testing, the effects of guilds is shown in the second column. Significant effects are indicated in bold (d.f. = estimated degree of freedoms, *F* = *F* value, ***$P < 0.001$, **$P < 0.01$). Significant difference (interaction) between the guilds is shaded gray.

Fruit body size and environmental factors

At the assemblage level, fruit body size was significantly influenced by temperature seasonality, annual mean temperature, eNPP and total biomass (Model 3, Table 2, Fig. 4). At the cross-species level, fruit body size for both guilds was significantly influenced by temperature seasonality (Model 4, Table 2). ECM fungi additionally showed a significant relationship with temperature (Table 2). Between guilds, the curve shapes of temperature seasonality, eNPP and annual mean temperature were significantly different (Table 2). A cross-species model for all guilds supported the importance of both temperature seasonality and annual mean temperature as significant factors (Table SR2, Fig. SR9). Overall, the shapes of the observed relationships were consistent with the seasonal resource surplus hypothesis and the heat-up-cool-down hypothesis but not the ecosystems biomass hypothesis (Fig. 2B).

DISCUSSION

The macroecology of size-related traits is well developed for animals (Bergmann 1847; Chown & Gaston 2010) and plants (Moles *et al.* 2009) whereas this study is the first macroecological assessment of the variation of an important fungal trait, fruit body size. Our analysis revealed a hump-shaped relationship between the mean fruit body size of mushroom-forming fungi and the distance to the equator, and that the largest fruit bodies occurred in areas characterised by a high seasonality as well as an intermediate annual mean temperature. These results are consistent with both the resource availability hypothesis and the thermoregulation hypothesis. Overall, the responses of mutualistic ECM and SAP fungi were similar, indicative of common constraints on fruit body size regardless of lifestyle and energy source. In addition, our findings supported those of previous studies, in which larger mean fruit body sizes in ECM than in SAP fungal communities were reported (Bässler *et al.* 2015). The patterns identified herein differed fundamentally from those of other sessile organisms such as plants, which are tallest at low latitudes due to the high amounts of precipitation during the wettest months (Moles *et al.* 2009). In plants, seed size decreases with latitude,

which has been attributed to changes in plant growth forms and vegetation types (Moles *et al.* 2007).

Environmental drivers of global fruit body size

The absence of a significant positive correlation between fruit body size and total ecosystem biomass contradicted the findings of a local study (Bässler *et al.* 2016) and thus suggested that the relative importance of environmental drivers of fruit body size changes with the spatial scale. The specific characteristics of the tropics, particularly their large biomass and, on average, small fruit bodies, may explain the lack of a positive relationship between fruit body size and ecosystem biomass. Although not covered by our hypotheses, the small size of fruit bodies at lower latitudes reduces their exposure to unfavourable conditions, as the time span needed to develop and produce spores is shorter (Halbwachs *et al.* 2016). Hence, in warm, humid tropical systems, where microbial, pathogenic and predation pressures are commonplace (Bahram *et al.* 2018; Halbwachs & Simmel 2018), small, short-lived fruit bodies would likely be an advantage.

Mycelial size in tropical systems may also be limited due to competition for soil nutrients with microbes, such as bacteria or even other fungal species (Zhu *et al.* 2016). Repeated fungal exposure to ephemeral and fluctuating resources would lead to the evolution of small mycelia and an upper size limit for the production of fruit bodies. Competition for resources is generally more intense in tropical than in temperate and boreal systems (Ruan *et al.* 2004). While the generally nutrient-poor soil at low latitudes could also lead to size constraints in mushroom communities, the lack of a consistent effect of soil fertility across our models suggests that soil fertility is of minor importance in the evolution of fruit body size. Instead, it may be that within the productive tropics, and as noted above, there is a selection towards species able to avoid pathogenic and other pressures by reducing their exposure time, such as by producing small fruit bodies.

Both climate seasonality and eNPP were selected to examine the seasonal resource surplus hypothesis, as they have also been used to explain large-scale patterns of animal body size, abundance and diversity (e.g. Williams & Middleton 2008; Huston & Wolverton 2009; Huston & Wolverton 2011). Both variables reflect the temporal availability of resources. While climate seasonality mainly determines the temporal (seasonal) access to resources during a year via favourable temperature and/or moisture conditions, eNPP mainly reflects the amount of resources available relative to the time they can be used by a given species. Across models, the effects of climate seasonality on fruit body size were stronger than those of eNPP. Nevertheless, for most response variables, particularly at assemblage level, eNPP was also positively related to fruit body size, thus explaining the independent variability of the latter. However, our results suggest that in terms of fruit body size, the temporal access to resources is more important than the total amount of resources available for metabolism. This temporal access may favour species with large fruit bodies for two reasons: The first involves morphological opportunities, as the ratio between the hymenium (spore producing area) and fruit body biomass is higher for a few large than for
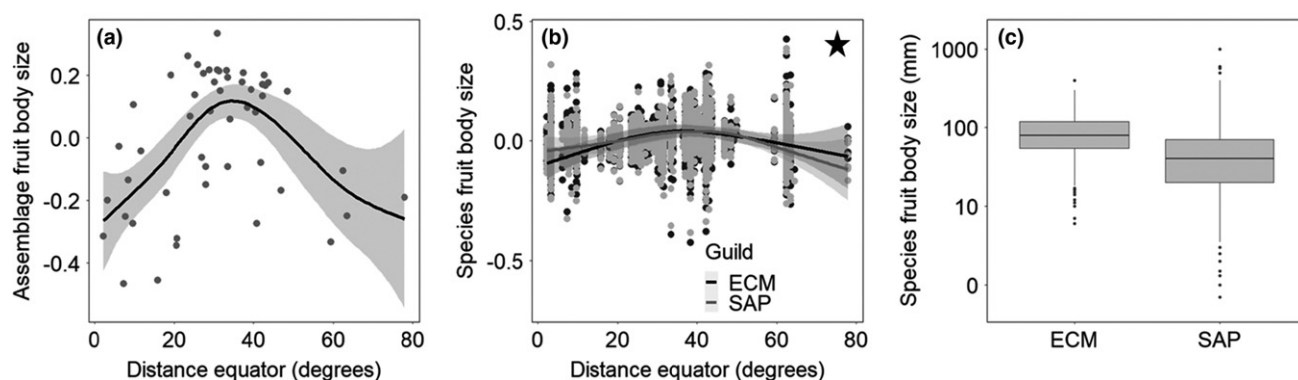
Figure 3 Fruit body size vs. distance to the equator, and species fruit body size for the two guilds (a) Effect of fruit body size at the assemblage level with a curve represented by a thin plate regression spline as a function of the distance to the equator (Statistical methods, Model 1). (b) Effects of species fruit body size at the cross-species level with a curve represented by a thin plate regression spline as a function of the distance to the equator (Statistical methods, Model 2). The effect was estimated separately for ectomycorrhizal (ECM) and saprotrophic (SAP) fungi. The star in the upper right corner indicates a significant difference in the curve shapes between guilds. Fitted curves in A and B as well as shaded areas represent the fitted smooth ± 2 standard errors. (c) Boxplots (median, hinges correspond to the 25th and 75th percentiles; the upper/lower whisker extends from the hinge to the largest/smallest value that is no further than 1.5 * IQR (interquartile range) from the hinge and outlying points) showing the differences in the species fruit body size within ECM and SAP guilds. The difference in species fruit body size between guilds was significant (see Tables 1 and 2).

Table 2 Environmental models

| | | Ressource availability | | | | | | | | Thermal conditions | | |
| | | Total biomass | | Temperature seasonality | | Precipitation seasonality | | eNPP | | Temperature | | |
	Guild: ECM *t*-value	d.f.	F	d.f.	F	d.f.	F	d.f.	F	d.f.	F	Adj. R^2
Assemblage level	All	1.00	**4.73***	1.00	**20.06*****	1.39	0.08	1.00	**5.15***	3.26	**6.86****	0.54
Cross-species level	ECM	−8.90***	0.89	1.17	**5.63***	1.32	0.11	1.00	0.003	3.06	**3.81****	0.23
	SAP		1.49	1.00	**10.06****	3.21	1.70	3.41	1.78	2.36	2.17	

Results of the generalised additive models of fruit body size vs. environmental variables at the assemblage (Statistical methods, Model 3) and cross-species (Statistical methods, Model 4) levels. The cross-species approach also included the guild (ECM = ectomycorrhizal and SAP = saprotrophic). The reference group for simultaneously testing the effects of the two guilds is shown in the second column. Significant effects are indicated in bold (d.f. = estimated degree of freedoms, F = F value, ***P < 0.001, **P < 0.01, *P < 0.05). Significant differences (interaction) between the guilds are shaded gray.

many small fruit bodies (Halbwachs *et al.* 2018). The second is temporal opportunities, as large fruit bodies have a generally longer life expectancy, often with several sporulation events (Halbwachs *et al.* 2016). Why eNPP explains fruit body size to a lesser extent than temperature seasonality is unclear. However, since for many of our localities their fungal lists cover a very large scale, with no information on the exact locality of the fungal records (Fig. SM1), eNPP may vary substantially within the large polygons due to soil-related factors. Thus, the calculation of a mean eNPP for each polygon may cause a stronger leveling-off of the effects of eNPP compared to those of temperature seasonality. Further studies are needed that include direct, detailed measurements of seasonal surplus and resource use.

The hump-shaped relationship between fruit body size and annual mean temperature suggests that thermoregulatory effects on fruiting bodies in part explain the large-scale pattern of trait variation across fungal assemblages. Cold and heat stress avoidance by the fruit body is likely to involve rapid heating-up and cooling-down mechanisms rather than

thermal conservation (buffering large fruit bodies against heat and cold stress). A further explanation, relevant for species with small fruit bodies at high latitudes, is the need to escape freezing. Soft-fleshed mushrooms in boreal and arctic ecosystems are at high risk of freezing during fructification and spore production (Halbwachs & Simmel 2018). With small fruit bodies, spores are produced within a short time frame such that the risk of damage induced by freezing is minimised. Other potential mechanisms should be explored in further studies. For example a large fruit body might also be at an advantage in dry environments due to a reduced loss of water, as proposed for insects (Remmert 1969). This mechanism could also lead to a hump-shaped relationship with latitude, caused by the humid tropics and by a smaller evaporative water loss in cold northern habitats. On the other hand, most mushrooms possess a cutis (skin of the cap) of varying thickness that protects them against desiccation (Halbwachs *et al.* 2016).

In an earlier study, we showed that fruit body size is larger in ECM than in SAP fungi at local and regional (northern
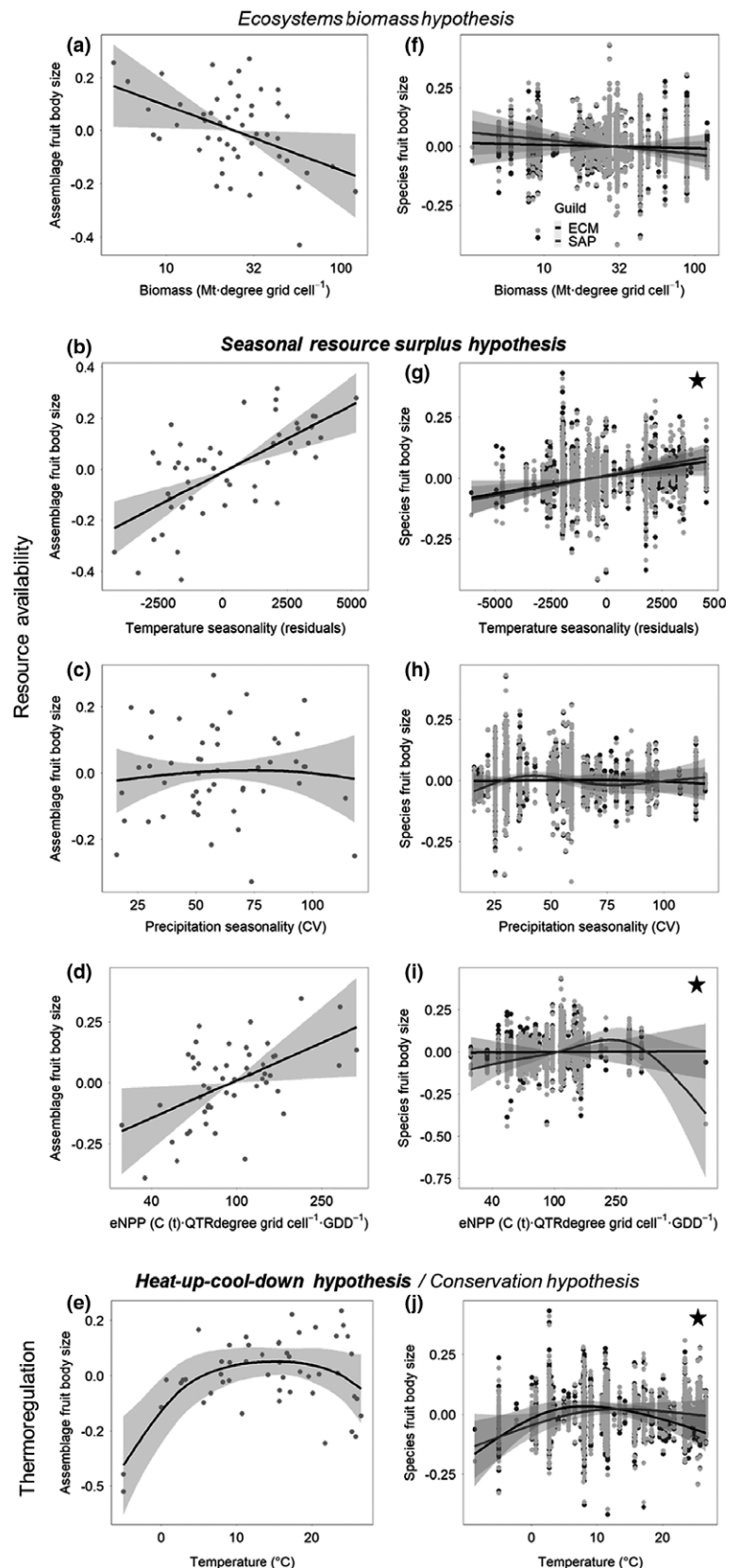
Figure 4 Fruit body size vs. environmental factors. (a–e). Partial effect of fruit body size at the assemblage level with a curve represented by a thin plate regression spline as a function of the environmental variables (Statistical methods, Model 3). (f–j) Partial effects of species fruit body size at the cross-species level with a curve represented by a thin plate regression spline as a function of the environmental variables (Statistical methods, Model 4). Partial effects were estimated separately for ectomycorrhizal (ECM) and saprotrophic (SAP) species. The star in the upper right corner indicates a significant difference in the curve shapes between guilds. The hypotheses in bold were supported by the data (Fig. 2b). Shaded areas represent the fitted smooth ± 2 standard errors.

Europe) scales (Bässler *et al.* 2015). This study expands this observation to a global scale. Assuming that fruit body size is related to mycelial size, our observation supports the view

that the evolution of a mutualistic lifestyle does not only lead to larger body size but also to larger modules (Seeman & Nahrung 2018). Overall, more field and laboratory studies are

needed to shed light on the relationship between temperature, moisture stress and lifestyle with respect to fungal fruit body size.

CONCLUSIONS

Fungi are the forgotten kingdom in macroecology, despite their ecological relevance in most ecosystems. While size-related functional traits have been extensively explored in animals and plants, ours is the first study to focus on the latitudinal and environmental responses of fungal fruit body size on a global scale. Fruit body size is a central trait for reproduction and dispersal in fungi. Our results suggest that resource availability (seasonal resource surplus hypothesis) and thermoregulation (heat-up-cool-down hypothesis) are major drivers of fruit body size. Although the data set was too limited for an evaluation of the relative importance of these vs. other potential drivers, our findings highlight the importance of the direct and indirect effects of mean and seasonal temperature, the consequences of which are especially relevant for global fungal assembly patterns in times of climate change. Nevertheless, the limitations of our data set call for further studies to explore the importance of traits as predictors of the response of species to climate change.

AUTHORS' CONTRIBUTION

CB, HH and RB conceived the study. HH surveyed the literature data. CB and RB designed the study and planned analyses. CB analysed the data and wrote the manuscript. RB and HH helped to refine and focus the writing and data interpretation. JM, FK and AR commented on drafts of the manuscript.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13678.

DATA AVAILABILITY STATEMENT

All data analysed as part of this study are included in this published article and its supporting information files and will be archived in the public repository Dryad https://doi.org/10.5061/dryad.2fqz612ng.

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