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EDITED BY

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University of Haifa, Israel
David Wilkinson,
University of Lincoln, United Kingdom

*CORRESPONDENCE

Franz-Sebastian Krah
✉ krah@uni-bayreuth.de

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The unresolved ecological and evolutionary role of fungal fruit body coloration

Franz-Sebastian Krah ^{1,2*}

¹Fungal Ecology and BayCEER, University of Bayreuth, Bayreuth, Germany, ²Department of Climate Change Impacts on Agroecosystems, Global Change Research Institute of the Czech Academy of Sciences, Brno, Czechia

Fruit body-forming fungi are hyperdiverse and of central importance for the functioning of ecosystems worldwide. They provide habitat and resources for other organisms and perform critical roles in carbon and nutrient cycling. Like in animals and plants, fungal coloration is expected to play a fundamental role in response to biotic and abiotic environments, thus providing invaluable information to predict fungal and associated diversity in the Anthropocene. Despite centuries of plant and animal coloration research, the role of fruit body colors in fungal ecology remains mostly obscure. Essential questions are unresolved, such as: How do fruit body colors function to cope with abiotic stress? Do fruit body colors function to attract dispersal vectors or prevent predation via camouflage or aposematism? What is the significance of fruit body colors for fungal fitness? What are the implications of climate change-induced fruit body color change on fungal and associated biodiversity? Here, I review existing knowledge and outline several research trajectories to better understand the ecological role of fruit body colors. Revealing climate-driven adaptations and interactions with other organisms will improve forecasts under climate change for fungal diversity and interrelated biodiversity and inform cross-taxonomic conservation strategies.

KEYWORDS

fungi–animal interactions, climate change, attraction, aposematism, camouflage, thermoregulation, defense, reflectance

Introduction

Fungi constitute one of the largest groups of organisms on Earth (Niskanen et al., 2023). They are crucial in carbon and nutrient cycling, providing ecosystem stability (Liu et al., 2022). Fruit body-forming fungi have evolved unique decay abilities (Floudas et al., 2012) as well as plant symbioses (Kohler et al., 2015) and provide resources to other organisms for breeding (Lunde et al., 2022) or nutrition (Fogel and Trappe, 1978; Elliott et al., 2022; Kitabayashi et al., 2022). Gaining a mechanistic understanding of the biotic and abiotic drivers of biodiversity is fundamental to forecasting and predicting fungal species and community performance and associated diversity in climate change (Urban et al.,

2016). Forecasts of biodiversity have implications for the management of protected areas (Hannah, 2010), conservation strategies (Dawson et al., 2011), and policymaking (Watson et al., 2019). Functional traits and experiments allow for a mechanistic understanding of species' adaptations to their environment and thus provide a better basis for forecasts than species diversity measures (McGill et al., 2006; Urban et al., 2016). Coloration, one of the most important functional traits on earth (Cuthill et al., 2017), is a complex trait with multifunctional roles as a visual signal and as pigments. Biotic processes include attraction, camouflage, aposematism, mimicry (Chittka and Raine, 2006), microbial defense (Narsing Rao et al., 2017), and dispersal (Lomáscolo et al., 2010). Abiotic processes include protection from abiotic stress such as extreme temperatures via thermoregulation (Trullas et al., 2007; Delhey, 2019), UV radiation, desiccation, physical damage, or heavy metals (Gill and Tuteja, 2010; Vavricka et al., 2010; Cordero and Casadevall, 2017). However, despite the enormous research on color in animals and plants (Chittka and Menzel, 1992; Caro, 2017; Cuthill et al., 2017), we lack even the most fundamental understanding of the multifunctional ecological roles of fruit body colors and, therefore, knowledge of the consequences of climate change for fungi and the biodiversity depending on fruit body formation. Fruit bodies are the organ of sexual reproduction of ca. 26,000 fungal species only within the Agaricomycetes (Sánchez-García et al., 2020). Their colors are important features in the systematic research (Guarro et al., 1999), species identification (Læssøe and Petersen, 2019), and the industry (Afroz Toma et al., 2023).

Pigments and colors in fruit bodies

Pigments found in fruit bodies are mainly melanins (dark brown), carotenoids (orange, yellow, and red), and betalains (yellow, red, and violet) (Gill, 1999; Velíšek and Cejpek, 2011). Fruit body colors are mainly brownish or whitish, but many fruit bodies are also brightly red, yellow, purple, or greenish (Figure 1A). These colors are, however, based on human vision color models and do not capture what other organisms might interpret. Currently, there are no studies of fruit body reflectance spectra (except some single species) (Bekiaris et al., 2020), and therefore, a respective database is missing, which also restricts the translation of fruit body reflectance into different color vision models, e.g., of beetles and mammals. Furthermore, it is currently largely unclear how frequently fruit bodies reflect in the ultraviolet range. Although structural colors seem to be absent (Brodie et al., 2021), fluorescence appears to play some role (Reinhold, 2020). Thus, a critical step will be to generate a fruit body reflectance database and use it to calculate textual colors for different organism visual models.

The diversity of colors is high among species; however, it may also be high among populations. Currently, we have generally only little information about the role of intraspecific trait variability in fungi (Krah and Bässler, 2021). Field identification guides often list the occurrence of varieties within species, which often differ in color (e.g., Knudsen and Vesterholt, 2008). There is currently no systematic assessment of color variability within species; however,

a recent publication found that the high color diversity in *Boletus edulis* could be partly explained by the population structure (Tremble et al., 2023). Thus, when fruit body reflectances are measured, the variability within the species should ideally be captured.

Biotic and abiotic factors

Both biotic and abiotic environmental factors relate to the coloration of organisms (Figure 1B).

Biotic factors

Within animal and plant studies, biotic mechanisms include attraction (e.g., pollinators, dispersers, and mating partners), aposematism and mimicry (e.g., repellence of consumers), camouflage (e.g., avoidance of consumers) (e.g., outlined in Caro, 2017), and antimicrobial activities (Cordero and Casadevall, 2017). First, fungus–animal interactions are frequent, including the utilization of fruit bodies as a food source by mammals and slugs, as a breeding ground for beetles and flies, or simply as a resting site for flying insects (Elliott et al., 2022; Borgmann-Winter et al., 2023). Attraction might play a role in dispersing sexual spores produced in the fruit body. Many studies have indeed suggested that animals may contribute to spore dispersal likely on small spatial scales (Guevara and Dirzo, 1999; Lilleskov and Bruns, 2005; Seibold et al., 2019; Elliott et al., 2022; Borgmann-Winter et al., 2023); however, wind dispersal is relevant for both short- and long-distance dispersal (Finlay and Clarke, 1999; Hallenberg and Kuffer, 2001; Galante et al., 2011; Golan and Pringle, 2017). Furthermore, the attraction could also signal profitability, similar to the color change of plant fruits when ripe (Sinnott-Armstrong et al., 2021). Although studies have shown that the nutritional value of fruit bodies varies with their developmental stages (Cheung, 2013), we do not know if, e.g., dietary fiber content correlates with color changes. Finally, fruit body color has been suggested as a warning (aposematism) of their unprofitability or poisoning to herbivores. First, we currently need more observational data on repellent tastes and toxic properties (but see below on antimicrobial defense) and only some reports and speculations for single species (Halbwachs et al., 2016). Second, textual color categories based on human color sensitivity did not correlate with human-coded unprofitability (Sherratt et al., 2005). The latter paper found a strong correlation between color and spore size, indicating a role of color in dispersal by insects or mammals. Thus, the correlation between spore size and fruit body color should be examined in more detail. The paper further suggested relations between smell and poisoning, highlighting the need to investigate olfactory clues when studying fungal colors. These results highlight that we need to understand whether fruit body color provides biotic signaling leading to increased or decreased animal consumption or visitations.

Although attraction is important in plant–pollinator interactions, other biotic factors may play a role. Based on the human color model, ca. more than 50% of fruit body colors are

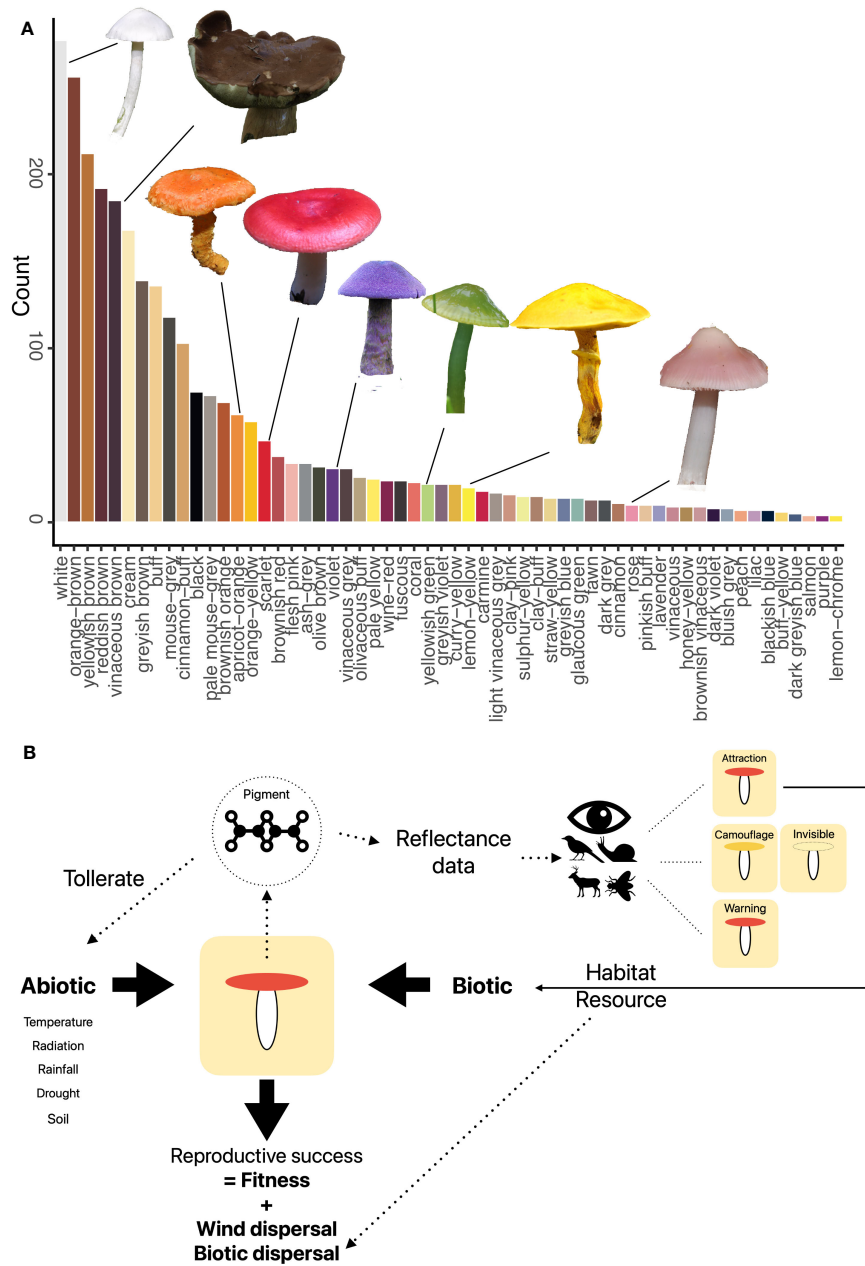


FIGURE 1
(A) Fruit body colors of 1,575 temperate fungal species based on a standardized color palette (Læssøe & Petersen, 2019). Fruit body images by Franz Krah. **(B)** Conceptual framework of the abiotic and biotic aspects of potential relevancy for the role of fruit body colors. Pigment production is driven by pigments, which also mediate responses to abiotic stress. Depending on the visual system, different colors are seen, which may lead to different animal behavior such as predation. Both abiotic and biotic factors may effect fungal fitness if they suppress maturation and spore release.

somewhat dull colored (Figure 1A), maybe resembling forest floors, especially in fall, when most species produce fruit bodies in the northern hemisphere (Krah et al., 2023). Visual camouflage could deceive mycophores and protect fruit bodies by preventing detection (crypsis) against the background or their substrates or environments (Stevens and Merilaita, 2009). The matching of fruit bodies with their backgrounds may thus prevent detection. Since the key function of the fruit body is protecting spore production until the release of spores, camouflage could protect the fruit body long enough to avoid being consumed before spore discharge

(Halbwachs et al., 2016; Nagy et al., 2017). However, the camouflage hypothesis has yet to be tested. Crypsis became known first in plants, where ca. 25% of all species are estimated to be cryptic or aposematic (Lev-Yadun, 2016). In fact, the lines between crypsis and aposematism are often not clear and many fruit bodies may be camouflaged and poisonous at the same time. In summary, we lack evidence in favor of or against the attraction and camouflage hypotheses.

Besides biotic factors based on visual signals, pigments may also play essential roles in the defense from bacterial and fungal attacks.

Those may include aspects of aposematism or the killing of pathogens and predators. Chemical defense strategies have been reviewed elsewhere (e.g., Spitteller, 2015). For example, the pigment mycenaaurin produced by the orange-colored species *Mycena aurantiomarginata* exhibits antibacterial activity (Jaeger and Spitteller, 2010); however, the ecological significance is still unclear. Another largely unexplored topic is photoactivated defense strategies. Many basidiomycete pigments show structural similarity with plant pigments, which are known for light-activated defense strategies such as the production of radical oxygen species (Siewert, 2021). A first case study showed that some pigments of species of *Cortinarius* subgenus *Dermocybe* are photoactivated and had toxic effects on a glassworm species (Hannecker et al., 2023).

Abiotic factors

Besides biotic factors, the abiotic environment also interacts with color, specifically pigments. Pigments have been described for some species (Gill, 1999), primarily for food and medicinal (Kalra et al., 2020) or for taxonomic and systematic purposes (e.g., Lodge et al., 2014). However, we need pigment composition data for most species (but see Siewert, 2021).

One of the most studied abiotic aspects of color is thermoregulation. The thermal-melanism hypothesis for ectotherm organisms, such as fungi, states that dark-colored organisms are at an advantage in colder environments (Trullas et al., 2007). Using the first large-scale fruit body distribution dataset, colleagues and I found that fungal assemblages had, on average, darker fruit bodies in colder environments, supporting the thermal-melanism hypothesis for the fruit body-forming fungi (Krah et al., 2019). In subsequent studies, this finding was confirmed along with an elevational gradient and independent from the microclimate (Krah et al., 2022; Oechler and Krah, 2022). Further hypotheses regarding fruit body coloration are the desiccation-protection hypothesis (DPH; Oechler and Krah, 2022), which predicts color adaptations of organisms in dry environments, and the photo-protection hypothesis (PPH; Rensch, 1929), which predicts color adaptations of organisms in radiation-rich environments. Considering multiple covariates, Krah et al. (2019) found no support that darker colors are related to radiation protection but that assemblage color lightness varied with precipitation, maybe due to desiccation protection via pigments (Cordero and Casadevall, 2017). Despite these first vital insights, we still need to find out whether fungi respond plastically in terms of fruit body pigmentation to environmental factors, whether pigmentation can reduce environmental stress, and whether pigmentation provides a fitness benefit in specific conditions such as biomass or number of viable spores. Thus, additional studies relating measured color spectra and pigment composition to abiotic factors and testing for fitness advantage under controlled conditions are needed.

Besides ecological studies, phylogenetic comparative methods also provide important insights into the ecology and evolution of

coloration. For example, plant species likely diversified in co-evolution with pollinating insects (van der Niet et al., 2014). In Agaricomycetes, only low phylogenetic signal of color lightness was found across ca. 3,000 species, suggesting rather adaptive evolution of pigments and colors (Krah et al., 2019). However, the low phylogenetic signal may also have resulted from considering only one aspect of color in terms of color lightness.

Future perspective

The summary of studies clearly shows a need for more research on the role of fruit body coloration in fungal ecology. Thus, in the following, I will highlight essential ways forward toward research trajectories required to fill the apparent research gaps. Those will include generating novel data and combining them with existing data to address macroecological questions. Furthermore, laboratory and field experiments are needed to test for abiotic effects on color and explicitly test for attraction/aposematism vs. camouflage. These studies should be complemented by functional and physiological studies focusing on how color mediates fungal responses to their environment and fitness.

Database and color models

The current greatest obstacle in studying the role of color in fruit bodies is the need for more data on fruit body reflectance spectra. Thus, research efforts should increase to measure reflectance. Furthermore, reflectance should be translated into different color vision models. Insects, mammals, birds, and slugs are relevant for fungi-animal interactions (Elliott et al., 2022). For instance, most mammals have two photoreceptors sensitive to green and blue light (Jacobs, 2009); most insects have either three or four photoreceptors sensitive to UV, blue, and green light, for example, the honey bee or flies, respectively (Backhaus, 1991; Lunau, 2014; Hannah et al., 2019); however, many beetles possess two photoreceptors, which is also likely true for Staphilinidae (beetles often found in fruit bodies), but some beetles have four photoreceptors (van der Kooij et al., 2021); birds have four kinds of photoreceptors sensitive to red, blue, and green light and some are also sensitive to UV (Hart and Hunt, 2007); the visual system of slugs is most likely not able to differentiate colors due to their reduced optical system and their mostly nocturnal activity (Dimock Jr and Parno, 1981; Nishiyama et al., 2019).

Big data integration

Macroecological community ecological approaches have proved invaluable in ecological research in testing broad species diversity and functional diversity patterns (Keith et al., 2012). Utilizing large datasets, macroecological community patterns can inform about the relative effects of different predictor sets while incorporating a large

volume of existing diversity. Despite their correlative nature, the large amount of data used provides robust statistical means to gain first insights into ecological relations that are of importance to inform more detailed analyses and experiments. Existing extensive species distribution datasets that draw from reputable sources such as the CLIMFUN project (Andrew et al., 2017; Krah et al., 2019), GBIF (GBIF, 2017; Krah et al., 2023), and GlobalFungi (Větrovský et al., 2020) should be integrated with reflectance measurements to build macroecological models and test for the relative importance of abiotic and biotic predictor sets (e.g., Dalrymple et al., 2020). Additionally, fungi–animal datasets in combination with reflectance data should be exploited. One example is the dataset comprising 58 fungal species, 40 insect species (Cisidae), and 65,675 interaction data points (Reibnitz, 1999), which was used prior to studying fungi–insect relationships, but without consideration of color traits (Thorn et al., 2015). In addition, several articles exist where feces were collected and fungi were identified via metagenomic approaches (Bradshaw et al., 2022; Kitabayashi et al., 2022; Ogórek et al., 2022; Weinstein et al., 2022); however, these data have not been analyzed yet in terms of the fruit body coloration. One promising approach might be to use the existing species-by-species fungus–animal associations and use occurrence data (e.g., GBIF) to test for phenological overlap of fruiting and, e.g., insect activity. Given enough temporal resolution of the data, it would be important to test for phenological mismatches over time, as this would be the first evidence for a novel form of mismatch that might be explained by climate warming.

Experiments

The attraction, aposematism, or camouflage hypothesis for fungi have not been tested in experimental settings. Therefore, real-world field experiments should be used to test the independent effects of fruit body traits on animal interactions. Furthermore, if the studied species are involved in fungus–animal interactions, color changes via abiotic factors may disrupt those interactions. One experiment could be designed to test if species with specific colors are more visited by animals. Fruit bodies could be treated in the field to disentangle a visual signal (color), an olfactory signal (volatiles), and abiotic factors by differentially excluding either the visual signal or the olfactory signal. This experiment could comprise fruit bodies of species and five treatments: (i) real fruit body, (ii) real fruit body covered by transparent odor-impermeable nylon-resin oven bag (visual only), (iii) only transparent odor-impermeable nylon-resin oven bag (visual control), (iv) real fruit body covered by odor-permeable intransparent green muslin bag (scent only), and (v) only odor-permeable intransparent green muslin bag (scent control). This approach has been successfully conducted within the plant–pollinator research (Policha et al., 2016). To identify insects and other animals, a camera survey (Schmid et al., 2019) or sticky traps (Graf et al., 2022) could be used.

Functional studies

Many of the pigments responsible for fruit body colors may have a role in resistance to abiotic stressors, including extremely high or low temperatures, low water availability, rainfall as physical damage, or ultraviolet radiation (Cordero and Casadevall, 2017). Depending on the pigment composition and the color spectra, species and individuals should be differentially able to exist in an environment more or less affected by such stressors. Thus, pigments and colors should provide a fitness advantage in harsher environments. To fully support any of the thermal-melanism, the DPH or the PPH requires three aspects to be supported (following Cordero et al., 2018): (1) colors are related to the specific abiotic variable (e.g., darker fruit bodies in colder environments), (2) colors function to reduce abiotic stress (e.g., darker fruit bodies warm faster than light-colored ones), and (3) colors provide a fitness advantage in the abiotic condition (e.g., darker fruit bodies have the same biomass in cold environments as light-colored ones in warm environments). Fruit bodies could be collected across different environments with measurements of dry weight and the number of spores determined as relative fitness. For the abiotic physiological stress experiments, fruit bodies could be subjected to high UV radiation followed by a spore viability test, or placed under an artificial solar radiation (Krah et al., 2021) to determine warming rates, or placed in a drying cabinet to determine desiccation rates.

Phylogenetics and evolution

Further phylogenetic analyses would be helpful to answer some important evolutionary questions. For example, how conserved pigments and colors are across larger phylogenies may inform about selective pressures. Furthermore, fungal diversification rates may be explained by the kind of fungus–animal interaction. Likewise, estimating precisely the first occurrence of certain pigments and colors can help to explain the mechanisms behind color pattern we see today.

Conclusion

The role of colors is a key trait with implications for fungi's relations to both the abiotic and the biotic world. Establishing a trait-based mechanistic understanding of how color mediates fungal responses to climate and other factors will enhance our ability to forecast fungi under global change. Furthermore, identifying the role of color in fungi–animal interactions will allow assessing the potential for climate change-induced disruption of their interaction via color change. Finally, a better understanding of the biology of fruit body colors will also benefit a more holistic understanding of color across kingdoms.

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