A mushroom by any other name would smell as sweet: *Dracula* orchids

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Abstract

Mimicry, like coral snakes and their nonvenomous imposters, is one of the most compelling examples of evolution by natural selection. Although mostly known from animals that gain protection by resembling an unpalatable or harmful compatriot, both types of mimicry, Müllerian and Batesian, also occur in plants and fungi. Some fungi are known to mimic flowers to dupe pollinators into vectoring spores or to achieve "pollination" themselves, but flowers that mimic fungi are highly unusual. However, in the cloud forests of the Neotropics, the orchid genus *Dracula* appears to be a remarkable example of a bizarre but successful fungal mimicry: Over 100 species have flowers that look and smell like fleshy mushrooms to attract pollinating flies. Although it has been speculated that *Dracula* orchids and some other flowers may mimic mushrooms as a way to access an abundant and untapped pollinator resource, until recently no empirical data have been gathered to investigate this hypothesis. Here we review what is known about the models (fleshy mushrooms), the mimics (*Dracula* orchids) and the "signal receivers" (fungus-seeking flies) that encompass this rare and fantastic phenomenon of mushroom mimicry. This knowledge base allows us to examine how the system came about, how it is sustained, and what might threaten its posterity. Critically, in the face of an increasing rate of habitat loss, the only way to preserve the threatened marvel of mushroom mimicry may be to make a concerted effort to preserve the native mushrooms.

Introduction

Mimicry, the adaptive resemblance of one organism to another, is one of the most compelling illustrations of the power of natural selection (Darwin 1859, Bates 1862, Wallace 1870, Poulton 1890, Fisher 1930, Gilbert 1983). Most examples of mimicry are from animals that exploit one another to gain protection from predators, yet mimicry also occurs in plants and fungi (Roy and Widmer 1999, Roy 1993). Unlike most animal mimicry systems, where the reproductive success (fitness) of mimics is a direct consequence of survival and is enhanced by their ability to deter predators, the fitness of plant and fungal mimics is a direct consequence of their ability to produce offspring and is enhanced by their ability to attract pollinators.

Although rare, there are a few well-known examples of fungi that mimic plants for their own benefit. Both mummy berry disease of blueberries (caused by the ascomycete *Monilia vaccinii-corymbosi*) and some rust fungi that infect *Boechera* (=*Arabis*) spp. (Brassicaceae) and *Euphorbia cyparissias* (*Puccinia arrhenatheri* and the *Uromyces pisi* species complex, respectively) attract pollinating insects by looking and smelling like flowers (Batra and Batra 1985, Roy 1993, Roy and Raguso 1997, Raguso and Roy 1998, Pfunder and Roy 2000). This floral mimicry can be so sophisticated that, at least in the case of *Puccinia*-infected *Boechera*, the "pseudoflowers" created by fungus-modified leaves are colored yellow like abundant co-occurring flowers, produce scents normally found in true flowers, and even produce a sugary nectar that rewards visiting insects (Roy 1993, Roy and Raguso 1997, Raguso and Roy 1998). In this case, for mating to occur the *Puccinia* rust requires the insect visitors to bring the sexual spores together, just like bringing pollen to the stigma in flowering plants. Thus, the insects actually "pollinate" the fungus! Such dependence on insects for sexual reproduction is probably quite rare in fungi (probably most common in the rusts) and this lack of sustained, reproductively stimulated intimacy may, in turn, explain why mimicry in fungi is exceptional. Consequently, examples of mimicry outside of the animal kingdom are best known from the largely insect-dependent flowering plants.

Both major types of mimicry found in animal systems, Müllerian and Batesian, can be observed in plants, especially the orchids (Bierzychudek 1981, Dafni 1984, Johnson 1994, Roy and Widmer 1999, Gigord et al. 2002). To understand how mimicry evolves in plants, it is important to understand the various mechanisms by which natural selection can produce such a sophisticated resemblance. Müllerian mimicry in plants is when two or more flowers coevolve to look like a single type of flower, which is the product of enhanced pollinator visitation to both plants because they look like a single, large reward for the pollinators. This is an example of "positive frequency-dependent selection," which is when your ability to produce offspring is best when you are common (Futuyma 1998, Roy and Widmer 1999). On the other hand, Batesian floral mimicry entails the exploitation of a previously established pollinator-plant relationship by a deceitful mimic (Dafni and Ivri 1981, Roy 1993, Johnson 1994, 2000, Johnson et al. 2003). In some cases, floral Batesian mimics look like other insects rather than flowers to deceive male insects seeking female mates (Dafni 1984, Ackerman 1986, Dafni and Calder 1987, Blanco and Barboza 2005). Batesian mimicry is thought to be an example of "inverse (negative) frequency-dependent selection" where it is best to be rare because if you are common, the duped insect will learn to avoid you (Futuyma 1996, Roy and Widmer 1999). Because Müllerian mimicry is often less specific, Batesian mimicry is probably responsible for the most extreme cases of resemblance within the plant kingdom. In fact, Batesian mimicry has been suggested to be an explanation for the success of deceptive pollination strategies in orchids (Roy and Widmer 1999, Gigord et al. 2002), which occurs in roughly a third of the 30,000 known species (Ledford 2007), suggesting that Batesian mimicry may be one of the principal forces driving orchid diversity. And just like the fungi that mimic flowers, some plants appear to mimic fungi in order to attract pollinators.

Organisms that mimic fungi are almost unknown. Some insects use camouflage that includes the shape, pattern, and color of lichens on the surfaces of leaves and other substrates, probably because of their relative permanence in the landscape, but few reports exists of any organism's resemblance to ephemeral, fleshy fungi. Thus, the speculation that some flowers mimic mushrooms to attract fungus-seeking flies as pollinators (Vogel 1978, Vogel & Martens 2001) represents a highly unusual circumstance, even among fly-pollinated flowers (of which there are probably many). Some plants hypothesized to trick fungus-seeking flies by resembling a fungus to varying degrees include "Wild Ginger" (*Asarum* spp.) and the rare tree form of the "Dutchman's Pipe" (*Aristolochia arborea*), both of the family Aristolochiaceae, species of the genera *Arisarum* and *Arisaema* ("Jack-in-the-Pulpit" and allied taxa; Araceae), *Arachnitis uniflora* (which also subsists by taking sugars from fungi in the soil), and even the "Lady's Slipper" (*Cypripedium* spp.) and "Helmet Orchids" (*Corybas* spp., including recently segregated genera)(Vogel 1978, Vogel & Martens 2001). But one genus of Neotropical orchids, *Dracula*, takes the cake when it comes to the degree to which their flowers resemble mushrooms.

Dracula[1] is a genus of epiphytic orchid that produces flowers that look and smell like small mushrooms (Fig. 1). Most of these orchids exhibit a peculiar morphology of the lip-like lowermost petal of the flower ("labellum") that resembles the reproductive surfaces of gilled ("agaric") mushrooms (Vogel 1978, Dressler 1990, Luer 1993, Christensen 1994, Behar 1995, Kaiser 2006). In some species, such as *Dracula felix* (Fig. 1f), the outermost portions of the flower (sepals) have a superficial resemblance to the caps and stalks of small mushrooms. Most *Dracula* flowers are produced at the end of long stems and are oriented towards the ground where mushrooms are most abundant (Christensen 1994). Some of these orchids even produce scents reminiscent of fungi (Vogel 1978, Kaiser 1993, 2006). Chemical analysis of scents trapped from greenhouse-grown flowers of *Dracula chestertonii* show they are dominated by the long-chain alcohol 1-octen-3-ol and other "typical flavour compounds of mushrooms" (Kaiser 1993:31, Kaiser 2006). All of these floral traits are thought to function in *Dracula* for deceptive pollination by "fungus gnats" seeking places to lay their eggs (Vogel 1978, Christensen 1994), but the relative roles of the morphological and chemical cues in achieving pollinator visitation are not known. It is quite possible that these flowers combine imitations of multiple resources, such as places to take shelter during heavy rains or meeting places where potential mates can find each other (Jersáková et al. 2006). Furthermore, while it has been hypothesized numerous times that "fungus gnats" are the pollinators of *Dracula* species (Vogel 1978, Dressler 1990, Luer 1993, Christensen 1994, Behar 1995, Kaiser 2006), this hypothesis has only been confirmed recently with observations in their natural setting (Endara et al. 2010, Dentinger et al. unpubl.).

So, if these flowers are really mimicking mushrooms, which can only be confirmed with experiments that show the resemblance to be important to the flowers' ability to produce seeds, then what mushrooms are acting as the models, what are the flies doing at them, and why do these orchids mimic mushrooms? We have initiated studies of the ecology and evolution of *Dracula* using funds provided by the National Geographic Society and the National Science Foundation to get at these and other questions and we are only just beginning to unravel the intricacies of interactions among the models, mimics, and "signal receivers" in the bizarre world of mushroom mimicry.

The System

The models (gilled mushrooms?)

Given the spectacular resemblance of the *Dracula* labellum to the cap of a gilled mushroom, it follows that the models for this resemblance are likely to be agarics. Moreover, most *Dracula* labella are white, or white with reddish-purple ridges, further suggesting that the models may be white agarics with or without colored edges to the gills. We don't know yet if white agarics are the most common type of mushroom at our study site, but anecdotally this makes sense as it is common knowledge that the fleshy mushroom communities of moist Neotropical forests are dominated by litter- and wood-dwelling saprobes, which are often from the families Mycenaceae, Marasmiaceae, and the catch-all Tricholomataceae. On the one hand, the orchids could be mimicking specific co-occurring mushrooms, but it seems more likely that they are converging on an abstract "mushroomness." This mushroomness would

[1] The inventor of the genus, Carl Luer, explains that he chose the name, which means "little dragon," because many of the described species had specific epithets that refer the face-like appearance of the flowers to mythological monsters or bats (Luer 1979).

be defined by the types of mushrooms most frequently encountered by the pollinators as well as by the pollinators own perception of what a mushroom is (and these are probably related). How a small fly "sees" a mushroom may be very different than how we see it, so we have to be very careful as we explore this fundamental aspect of the mimicry system. For one thing, we suspect scent plays a critical role in how the flies find mushrooms, but the look and texture of the mushroom-like labellum may be what keeps them around the flower or entices them to land. We are testing these ideas using floral manipulation experiments where we cover flowers with bags that block the visual cues but allow scents to pass through freely. If scent is the primary attractant, then flies should visit bagged flowers. In the following years, we will also employ artificial flower models that vary in sizes, colors, and textures of their various components. In addition to these field experiments, we are also collecting and analyzing fragrances from naturally co-occurring flowers and mushrooms to see if their chemical compositions are the same. Complementing our scent collections, we are using synthetic fragrances to see how well they can attract pollinating insects in the absence of flowers. All of these experiments should help us understand how important the visual versus olfactory cues are to the fungus-seeking flies.

Unlike plants and animals, it is not clear if mushroom diversity is higher in tropical or temperate regions. Comprehensive studies evaluating fungal diversity in temperate versus tropical regions are lacking, even though the global estimate of fungal diversity is based on extrapolating the 6:1 ratio of fungi to plants in the British Isles to the enormous plant diversity in the tropics (Hawksworth 1991, 2001). Although there is a long list of taxonomically focused monographs and at least one attempt at a comprehensive floristic treatment for regions relevant to the cloud forests of Ecuador (e.g., Dennis 1970; Singer 1975, 1978), there are no detailed studies of the mushroom community in forests where these orchids occur (or anywhere, really!). The superb and recent work by Thomas Læssøe and colleagues (http://www.mycokey.com/Ecuador.html) has provided a start, but all of this work is only just scratching the surface of the enormous mushroom diversity that undoubtedly exists in Ecuador and other tropical countries. In January 2008, we made about 150 collections and have begun to identify them (Fig. 2), but this tedious task is made especially difficult by the lack of previous documentation in these forests as well as our frequent encounter with undescribed species. Many more collections need to be made before we will have a good idea of what and how many species occur there, but we have done enough preliminary collecting to begin to determine which species are frequent and which commonly co-occur with the orchids, at least during a single year's sampling. The ubiquitous families Mycenaceae and Marasmiaceae are definitely among the most common and abundant in these forests.

*The mimics (*Dracula *spp.)*

The genus *Dracula* was recognized on the basis of the distinct mushroom-like appearance of the labellum (Luer 1978). There are over 150 species of *Dracula* orchids, all of which are restricted to mountainous habitats of the Neotropics (Luer 1993). They range from southern Mexico (1 sp.) to Peru (1 sp.), and are most diverse in the Ecuadorian Andes (>40 spp.) and the western and central Colombian Andes (>60 spp., Luer, 1993). Some species of *Dracula* have widespread ranges (e.g., *D. vespertilio*, found from Nicaragua to Ecuador), while many are known only from single mountain valleys (Luer 1993). The plants grow on other plants (epiphytic) and occur only in undisturbed, old-growth cloud forests where there is ample humidity and indirect sunlight (Luer and Escobar 1988, Luer 1993).

Most species flower throughout the year with stems that successively produce single flowers, but some are known to flower only once a year (Luer 1993, L. Jost, pers. comm.). At our study site (see below), at least five abundant species flower during the rainy season, particularly January through March. One of the species, *D. felix*, is extremely common, flowers abundantly, and often has many (>20) flowers present at the same time (Fig. 1a). Although *Dracula* orchids mostly grow on trunks and branches of trees, they are frequently found on downed branches and logs, or even on the ground where they have fallen.

*The signal receivers (*Zygothrica *spp.?)*

The common visitors to four *Dracula* species in western Ecuador have been identified as flies in the genus *Zygothrica* (Diptera: Drosophilidae; L. Endara, pers. comm., Dentinger et al., unpubl.). While these small flies have been referred to as "fungus gnats" (Vogel 1978, Dressler 1990, Luer 1993, Christensen 1994, Behar 1995, Kaiser 2006, and L. Endara pers. com.), they belong to the fruit-fly family Drosophilidae, not the fungus gnat families Mycetophilidae or Sciaridae (Grimaldi and Engel 2005). We thus prefer to use the genus name instead of the inaccurate vernacular term "fungus gnat".

Zygothrica commonly utilize mushrooms at some stage in their life cycles (Grimaldi 1986), which is consistent with the observation that *Dracula* flowers function as visual and olfactory imitations of fungi to attract them (Kaiser 2006, Endara et al. 2010). Although the *Dracula* labellum has been interpreted as mimicking agarics, *Zygothrica* utilize several morphological "guilds" of fleshy mushrooms, including jelly fungi and pored mushrooms (Grimaldi 1986). A great deal of labellum variation occurs in *Dracula* (Luer 1993), so some species may be mimicking different types of mushrooms. This is a hypothesis we plan to test using synthetic models of orchid flowers that have different types of labella, recording the number and duration of pollinator visits to each type.

The relationship between *Zygothrica* and the mushrooms about which they aggregate is not yet clear. Few species appear to lay eggs in the mushrooms, three species have been seen grazing spores, and many utilize the mushroom caps for displaying stereotypical mating rituals (Grimaldi 1987). Thus, it seems most likely that these flies associate with mushrooms because they are used as "lekking" arenas, specific locations where males aggregate to display for sexually receptive females. Although the effects of each of these activities on the fitness of the mushrooms are unknown, using mushrooms as places to lay eggs, which is commonplace in fleshy mushrooms, may not have a negative impact if the fly larvae don't affect the mushroom's ability to produce spores, but it may also be parasitic if the larvae cause substantial damage (Corner 1972, Hackman and Meinander 1979, Bruns 1984, Hanski 1989). Grazing can be considered parasitic if all of the consumed spores are destroyed, but may also be beneficial to the fungus if some are expelled intact and the insect ends up dispersing them more widely (e.g, Lilleskov and Bruns 2005). Using mushrooms as lekking sites is unlikely to have a negative impact. Although the insect-mushroom relationship appears to range from casual (having no impact) to obligatory (parasitic/mutualistic), it is consistently intimate enough in at least some *Zygothrica* to be successfully exploited by perhaps more than 100 species of *Dracula* orchids. Could different species of *Zygothrica* utilize different types of mushrooms for lekking, thereby enabling the *Dracula* orchids to specialize on different pollinators and keep from mating with co-occurring orchid species? We are testing these ideas by using a common garden experiment where we arrange different *Dracula* species in a single location and observe pollinators to each. This allows us to eliminate the confounding effects of location on pollinator specificity. We are also observing fly behavior on both mushrooms and flowers using video cameras to document whether the behaviors are the same on both resources. Finally, we are collecting flies from both flowers and mushrooms to see if they are the same, and we are attempting to rear insect larvae from both mushrooms and flowers to see if the insects that lay eggs in either or both are the same as the pollinators.

Study Site

Our field work takes place at a private biological reserve (Los Cedros Reserve and Research Station; www.reservaloscedros.org), accessible only by mule, on the steep, muddy western slopes of the Andes Mountains in northwestern Ecuador, about 100 km as the toucan flies from Quito. The reserve encompasses 17,000 acres of rugged cloud forest (>84% untouched forest) ranging from 1000m to 2700m above sea level. The reserve serves as a buffer to the extensive Cotocachi-Cayapas Reserve in the Chocó Phyteographical Zone, well known as one of the most biodiverse regions on Earth, with an extraordinarily high level of species known only from this region. This location was chosen because of the relative ease of access (!) to a site that has high *Dracula* diversity in combination with the presence of sufficient facilities (including electricity) necessary to successfully carry out the extensive field research proposed for this project. This reserve is also dedicated to sustainable ecotourism that benefits the local indigenous community and to developing intercultural collaborations between visiting scientists and Ecuadorian students and researchers. This kind of coordination is crucial to long-term preservation of pristine habitat and promotion of productive collaborations between international research institutions.

Theoretical Considerations

Floral mimicry in plants evolves through selection of floral traits by pollinators. Pollinators will reinforce the evolution of mimics that appear more and more like the model. Changes in flowers that evolve to resemble other flowers are easy to comprehend because the floral parts are the same in the mimic and the model. For example, it's not too much of a stretch to imagine how one type of petal on one flower might change to look like another type of petal on another flower. But how does a flower become like a mushroom?

Based on the level of similarity shared between the mimic and the model, a mimic may be said to have either a "concrete" resemblance or an "abstract" resemblance to the model (Pasteur 1982). In concrete systems, the mimic imitates a single species or group of species, while in semi-abstract or abstract systems, the mimic imitates a virtual (e.g., protective eye spots on butterflies) or unidentifiable (e.g., threatening postures or colors that evoke fear) category (Pasteur 1982). In the case of fungal mimicry in *Dracula*, if the model is semi-abstract, i.e. "fleshy mushrooms," then the signal receiver must be able to respond to a diversity of signals that it may receive from all the variation produced by fleshy mushrooms. We suspect that *Dracula* orchids are not mimicking specific species of mushroom but are exploiting the innate preferences of *Zygothrica* for the most commonly encountered types of fleshy fungi in these habitats. But if this is true, then how do the various species of *Dracula* orchids that occur in the same location keep from reproducing with one another? One idea is that while the visual cues may be generalized, the fragrances are not, so that the orchids end up specializing on different pollinators because of differences in fragrances produced by both the flowers and by the mushrooms that the flies normally seek out.

There are few studies that have identified the critical factors that, to an insect, make a mushroom a mushroom (Jaenike 1978, Jaenike and Grimaldi 1983, Jaenike 1985). It is clear that different species of insect may utilize distinct parts of a mushroom or different stages of development, demonstrating the insects' discriminatory abilities (Bruns 1984, Jaenike and James 1991, Guevara and Dirzo 1999), but the relative roles of sight, scent, and touch in this discriminatory ability have not been sufficiently examined. Our research, which is attempting to elucidate the roles of these stimuli by observing fly behavior in response to each using flowers, mushrooms, and synthetic models, will reveal the signals that the insects receive from the mushrooms that, according to the flies, make mushrooms out of the flowers. That is, we will have a fly's perspective on "mushroomness." An understanding of this esoteric worldview is essential to understanding the ecology and evolution of mushroom mimicry in *Dracula*, and it is also vital if there is any hope of preserving these orchids and their cohorts in the face of impending threats to their natural environments.

Conservation

Conservation of mushrooms is *sine qua non* for any effort to preserve *Dracula* orchids in their native habitats. *Dracula* orchids only occur naturally in Neotropical cloud forests and as such are threatened by habitat loss through deforestation and global climate change. Because *Dracula* flowers are delicate and extremely sensitive to changes in temperature and humidity, they are dependent on undisturbed, exceedingly wet cloud forest. As land use changes and increasingly volatile weather patterns modify the environment, the natural conditions to which *Dracula* are adapted are lost or modified in a way that may never again support them. It is not known if *Dracula* can reestablish after disturbance. However, these orchids are not known to occur in regenerating forest and it is unlikely that they will colonize new, mature habitat without human intervention. A critical feature of *Dracula* conservation is acknowledging that their survival and persistence in the wild relies on the presence of pollinating insects, which, in turn, rely on the presence of fleshy mushrooms. We do not know yet how much the orchids rely on specific mushrooms known only from these forests, or if some other kind of exotic mushroom would be sufficient to reconstitute and maintain the mimicry, but it is likely that the mushrooms, insects, and orchids are tightly linked in a way that can only be successfully conserved by preserving the habitat in which they have evolved together. Critically, the dependence of *Dracula* on mushroom models that form the basis for this unusual mimicry highlights the need to specifically consider the conservation of mushrooms. This is perhaps the first case where the preservation of mushrooms is fundamental to the preservation of a charismatic icon of the tropical forest.

Conclusion

Mimicry of mushrooms is a rare phenomenon, if it exists at all. While it seems rather obvious from looking at *Dracula* flowers that they are mimicking mushrooms, couldn't it also be merely a coincidence? Surprisingly, no one has ever tested the hypothesis of mushroom mimicry (that the resemblance to a mushroom means they produce more offspring), in this or any of the other flowering plants hypothesized to be fungal mimics. In part, it is because testing this hypothesis is exceedingly difficult: How do you determine if the resemblance is the result of greater production of offspring? One way is by determining if the mimic produces more offspring if it is mixed in with the models (Roy and Widmer 1999). The idea here is that the signal receivers are less likely to recognize a non-rewarding mimic in the context of many rewarding models because selection will favor mimics that are indistinguishable from models (but if the senses of the signal receiver are keen enough, the *opposite* may be true if the mimicry isn't perfect). We are attempting to execute this test by manipulating the presence and absence of mushrooms around orchids and looking for changes in pollinator visitation, but this kind of manipulation is proving to be difficult because of challenges with establishing "model free" areas in natural habitat as well as the unpredictable nature of fly visitation – sometimes they are abundant and sometimes they are not. There are also logical conditions that must be met if it is true mimicry: The mimics and models must overlap in space and time and for long enough for the resemblance to evolve, the signal receivers must visit both the mimics and models, and the mimics must require visitation for reproduction (Roy and Widmer 1999). Some anecdotal evidence satisfies some of these requisite circumstances for *Dracula*, but it remains to be demonstrated that these orchids are truly mimicking mushrooms. And if it turns out they are not true mimics, then probably none of the other putative mushroom-resembling plants are, either. But given the spectacular resemblance of *Dracula* flowers in appearance, fragrance, timing, and location to mushrooms, as well as the empirical observation that they are pollinated by fungus-seeking flies (Endara et al. 2010, Dentinger et al. unpubl.), we suspect that these orchids really do smell as sweet as mushrooms, at least to a fly.

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Figure 1. Examples of *Dracula* orchids. A) *D. bella* (labellum), B) *D. carleuri*, C) *D. vespertilio*, D) *D. chestertonii*, E) *D. orientalis*, F) *D. felix*, G) *D. roezlii*, H) *D. inaequalis*. Scale bar is 10 mm and approximate based on published dimensions. All photos by Bryn Dentinger.

Figure 2. Potential models for the mimicry by *Dracula* orchids*.* A) *Chaetocalathus* sp., B) *Cheimonophyllum* sp., C) *Crinipellis* sp., D) *Xerulina chrysopepla*, E) *Hydropus* sp. F) *Filoboletus gracilis*, G) *Mycena* sp., H) *Marasmius* sp. Scale bar is 1 cm. All photos by Bryn Dentinger.