Coevolution of mushroom toxicity and animal consumer behavior

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Abstract. Fungal toxicity is increasingly viewed as an adaptive trait that evolved to deter or incapacitate animal consumers, thereby protecting reproductive structures and enhancing spore dispersal. This study examines the evolutionary interplay between toxic mushrooms and their consumers, addressing whether fungal toxins result from coevolutionary arms races or represent incidental byproducts of metabolism. Evidence from genomic and phylogenetic studies indicates that toxin biosynthesis, such as amatoxins in *Amanita*, *Galerina*, and *Lepiota*, has evolved independently multiple times, possibly through horizontal gene transfer. Behavioral and ecological data suggest that animal responses to fungal toxins vary widely, ranging from learned avoidance and social transmission of deterrent behaviors to potential physiological tolerance in larger mammals. However, direct evidence of genetic resistance among wild consumers remains limited. By integrating data from evolutionary biology, behavioral ecology, and toxin chemistry, this paper highlights the complexity of fungus-consumer interactions and identifies major knowledge gaps concerning the specificity and ecological function of fungal toxins. These insights contribute to a broader understanding of how chemical defense strategies shape cross-kingdom coevolutionary dynamics.

Key Words: animal behavior, coevolution, evolutionary arms race, fungal toxicity, fungivory, horizontal gene transfer, toxin resistance, mushroom toxins.

Introduction. Mushroom toxicity is widely hypothesized as an adaptive strategy in fungal life history: by deterring or incapacitating consumers, toxic fruiting bodies can survive long enough to disperse spores. In this sense, toxicity may serve the same role in fungi as plant secondary metabolites do in plants against herbivores. The diversity and potency of mushroom toxins, including those from genera such as *Amanita*, *Lepiota*, and *Galerina*, highlight the evolutionary significance of these compounds in deterring animal consumers and reducing predation pressure on reproductive structures (Govorushko et al 2019; Nieminen & Mustonen 2020; Li et al 2021). However, the effectiveness of this strategy is influenced by factors such as species identification challenges, environmental contamination, and the variable responses of animal consumers, which complicate the relationship between mushroom toxicity and consumer behavior (Govorushko et al 2019; Nieminen & Mustonen 2020; Liu et al 2022). Understanding these dynamics is crucial, as mushroom poisoning remains a significant public health concern globally, with both well-known and traditionally consumed species implicated in toxic incidents (Govorushko et al 2019; Nieminen & Mustonen 2020; Li et al 2021).

Purpose of the Study. The aim of this study is to explore the coevolutionary relationship between fungal toxicity and the behavior of animal consumers. Specifically, it investigates whether toxic secondary metabolites in mushrooms represent adaptive defenses against fungivory and how these compounds influence the evolution of avoidance, tolerance, or resistance among animal consumers. By integrating genomic, ecological, and behavioral evidence, the paper seeks to clarify the evolutionary origins and ecological functions of fungal toxins, assess the extent of reciprocal adaptations between fungi and their consumers, and identify key knowledge gaps in the understanding of these interactions. Ultimately, the study aims to contribute to a broader evolutionary framework explaining the diversity and persistence of toxic compounds in fungi.

Evolutionary Origins and Mechanisms

Independent origins and horizontal gene transfer. Highly toxic compounds like amatoxins (e.g., α-amanitin) are found in distantly related genera such as *Amanita*, *Galerina*, and *Lepiota*, suggesting independent evolutionary events and horizontal gene transfer (HGT) of toxin biosynthetic gene clusters (Luo et al 2018, 2022; Lüli et al 2019; He et al 2020). Recent genomic and phylogenetic studies show that the key genes for amatoxin biosynthesis, such as those encoding MSDIN precursor peptides and prolyl oligopeptidase B (POPB), form a monophyletic group across these genera, despite their distant evolutionary relationships. This is strong evidence for HGT (Luo et al 2018, 2022; Lüli et al 2019; He et al 2020). Here are some examples from genera *Amanita*, *Galerina*, and *Lepiota* (Table 1):

- *Amanita*: species like *Amanita phalloides* (death cap) and *A. virosa* are notorious for their high levels of α-amanitin and related toxins, causing most fatal mushroom poisonings worldwide (Sgambelluri et al 2014; Diaz 2018). *Amanita* species possess a diverse array of MSDIN genes, enabling the production of multiple cyclopeptide toxins (He et al 2020).
- *Galerina*: *Galerina marginata*, a wood-rotting fungus, also produces α-amanitin, with toxin levels sometimes rivaling those of *Amanita phalloides* (Enjalbert et al 2004; Luo et al 2012; Landry et al 2021). The biosynthetic pathway in *Galerina* is similar to *Amanita*, involving ribosomal synthesis and POPB-mediated macrocyclization (Luo et al 2012).
- *Lepiota*: several *Lepiota* species, such as *L. brunneoincarnata* and *L. venenata*, contain α-amanitin and related toxins, though the presence of these compounds is restricted to a monophyletic group within the genus (Sgambelluri et al 2014; Lüli et al 2019; He et al 2020; Sarawi et al 2021). Not all *Lepiota* species are toxic; for example, recent analyses found no amatoxins in *L. castanea* from Turkey (Yilmaz et al 2024).

Table 1

Amatoxin production in key genera

Genus	*Key species (examples)*	*Amatoxins present*	*Mechanism/genetic evidence*	*References*
Amanita	*A. phalloides*, *A. virosa*	Yes	Multiple MSDINs, POPB	Sgambelluri et al (2014); Diaz (2018); He et al (2020); Luo et al (2022)
Galerina	*G. marginata*	Yes	MSDIN, POPB, HGT	Enjalbert et al (2004); Luo et al (2012, 2014); Landry et al (2021)
Lepiota	*L. brunneoincarnata, L. venenata*	Yes	Monophyletic group, HGT	Sgambelluri et al (2014); Lüli et al (2019); He et al (2020); Sarawi et al (2021); Yilmaz et al (2024).

Mosaic evolution and arms race dynamics. Classic plant-herbivore coevolution models (Ehrlich-Raven) describe escalation cycles between toxin production and consumer resistance. Although most examples involve plants and insects, similar logic may extend to fungal toxins and fungivores: toxins evolve, consumer species adapt (behaviorally or physiologically), and fungi may escalate or diversify toxins in turn.

Recent research demonstrates that fungi can develop effective chemical defenses, such as toxin-producing endosymbionts, to deter fungivorous predators, and that these interactions can drive the maintenance and diversification of toxin production in fungal populations (Richter et al 2022). Experimental studies with yeast killer systems and parasitic fungi further support the existence of rapid, reciprocal coevolutionary dynamics, where increased toxin production in fungi is met with the evolution of resistance in consumers, followed by further escalation or diversification of fungal toxins (Joop & Vilcinskas 2016; Pieczynska et al 2016). These findings suggest that, much like in plant-herbivore systems, an evolutionary arms race shapes the diversity and potency of fungal toxins and the adaptive responses of their consumers (Joop & Vilcinskas 2016; Pieczynska et al 2016; Richter et al 2022).

Fungal Toxins and Consumer Behavior. Fungal toxins are hypothesized to deter consumers and protect reproductive structures, but the effectiveness and specificity of these defenses across animal groups remain complex and incompletely understood. Recent research highlights the diversity of fungal toxins, their variable impacts on invertebrates and mammals, and the challenges in linking toxin presence to consumer behavior and resistance.

Invertebrates and specialist fungivores. Many fungal toxins are specifically insecticidal or lethal to invertebrate fungivores, such as insects and slugs, which directly threaten developing sporocarps. Social insects, including ants and termites, have evolved behavioral and physiological adaptations, collectively termed "social immunity", to detect and avoid fungal toxins, reducing infection and poisoning risk at the colony level. Fungal toxins can trigger avoidance behaviors and activate innate immune responses in these insects, suggesting that toxins are a significant selective force shaping insect-fungus interactions (Liu et al 2019). However, the precise mechanisms and specificity of these defenses are still being elucidated.

Mammalian consumers. Evidence on mammalian responses to fungal toxins is limited. Some studies report that mammals, such as Japanese macaques, may exhibit taste hesitation or avoidance behaviors when encountering mushrooms, implying learned or innate aversion to toxic species. However, comprehensive data on behavioral or physiological resistance in wild mammals are scarce, and most available research focuses on human poisoning cases and laboratory animal models (Govorushko et al 2019; Nieminen & Mustonen 2020; Petrescu-Mag et al 2025). Experimental studies in mice have shown that high doses of both wild and cultivated mushrooms can cause elevated plasma creatine kinase and liver enzyme activities, but these effects often require large quantities and may not reflect natural consumption patterns (Nieminen et al 2005; Nieminen et al 2006; Nieminen et al 2008; Nieminen et al 2009; Nieminen & Mustonen 2020).

Tolerance in larger mammals. There are anecdotal reports that larger mammals (e.g., deer, squirrels) sometimes consume even highly toxic, amatoxin-producing mushrooms with minimal apparent effect. This observation raises the possibility that fungal toxicity may have evolved primarily as a defense against smaller vertebrates or invertebrates, rather than large mammals. However, systematic studies documenting genetic or physiological resistance in wild mammalian consumers are lacking (Nieminen & Mustonen 2020).

Coevolutionary Pathways & Modeling. Fungus-consumer interactions are shaped by complex coevolutionary dynamics, which do not always mirror classic one-to-one plant–

herbivore models. Recent research highlights both arms race and diffuse coevolution, as well as the roles of learning and social transmission in consumer responses to fungal toxins (Table 2).

Table 2

Current knowledge and hypotheses on fungal toxin evolution and consumer interactions

Aspect	*What is known*	*What is hypothesized or uncertain*
Toxin evolution	Independent origins; possible horizontal gene transfer of toxin genes	Defensive adaptation to fungivores, especially invertebrates
Consumer responses	Some mammals learn avoidance; invertebrate specialists sometimes deterred	Genetic resistance or sequestration in consumer species largely unproven
Coevolutionary dynamics	Models from plant systems apply conceptually	Evidence for fungal-consumer arms races remains indirect or theoretical
Learning vs innate aversion	Taste, bitter compounds, post-ingestive aversion documented	Innate avoidance traits or genetic selection for resistance uncharacterized

Arms race vs. diffuse coevolution. Fungus–consumer relationships often involve reciprocal adaptations, with evidence for both arms race dynamics (stepwise escalation of defenses and counter-defenses) and more diffuse, community-level coevolution. For example, studies of entomopathogenic fungi and their insect hosts reveal molecular arms races, where insects evolve chemical defenses (e.g., benzoquinone secretions) and fungi counter-adapt with detoxifying enzymes, such as benzoquinone oxidoreductases (Pedrini et al 2015; Joop & Vilcinskas 2016; Vilcinskas 2019). Experimental coevolution demonstrates that both hosts and pathogens can rapidly adapt, with the outcome depending on the diversity of interacting species and the specificity of their defenses (Joop & Vilcinskas 2016; Betts et al 2018; Vilcinskas 2019; Lievens et al 2024). Theoretical and empirical work in host-parasite systems shows that high parasite diversity can accelerate host adaptation and shift dynamics from fluctuating (Red Queen) to directional (arms race) selection, supporting the maintenance of toxin polymorphism when resistance evolves and production costs are balanced by reduced predation (Betts et al 2018; Märkle et al 2021; Lievens et al 2024).

Learning, innate aversion, and social transmission. Avoidance of fungal toxins by consumers can arise from both innate and learned behaviors. Animals may learn to avoid toxic fungi through direct experience (operant conditioning) or by associating illness with specific cues, as seen in amphibians learning to avoid pathogenic fungi after exposure (McMahon et al 2021; Poulton & Ellner 2025). Social transmission of avoidance behaviors, where individuals learn from observing conspecifics, can further reduce selective pressure for genetic resistance (Debiec & Olsson 2017). Neural and behavioral studies in both invertebrates and vertebrates demonstrate that aversive learning and memory extinction are mediated by conserved brain circuits, supporting the evolutionary importance of behavioral plasticity in toxin avoidance (Zhang et al 2018; Felsenberg et al 2018; Stelly et al 2019; Singh & Aballay 2019; Mondoloni et al 2022; Chiang et al 2022; Filipowicz et al 2022).

Evidence Gaps & Challenges. Despite advances in understanding fungal toxins, significant gaps remain regarding their ecological roles and the specificity of their interactions with animal consumers.

Sparse data on specific toxin-consumer pairings. Unlike the well-documented specificity in plant–insect systems, there are few studies that directly link particular

fungal toxins to specific consumer species and their tolerance or resistance mechanisms. Most research focuses on the general toxicological effects of mycotoxins in vertebrates and livestock, with limited experimental work on natural consumer–fungus pairings or the ecological consequences of toxin diversity (Trienens & Rohlfs 2011; Seyedmousavi et al 2018; Liu et al 2019; Awuchi et al 2022). This lack of detailed pairing data hinders our understanding of coevolutionary dynamics in natural settings.

Lack of documented genetic resistance in wild consumers. While herbivorous insects often evolve enzymatic detoxification pathways to cope with plant toxins, evidence for similar genetic resistance to fungal toxins in wild animal consumers is scarce. Experimental evolution studies in *Drosophila* show that insects can develop increased tolerance to fungal toxins, but this does not necessarily translate to true resistance or suppression of fungal growth, and such adaptations are rarely documented in wild populations (Trienens & Rohlfs 2011; Bosch et al 2017). In livestock and poultry, some detoxification mechanisms are known, but these are not always genetically based and may not reflect natural ecological interactions (Awuchi et al 2022; Hosseini et al 2023).

Confounding incidental toxicity. Some toxic fungal metabolites may arise as incidental byproducts of primary or secondary metabolism, rather than as adaptations for deterring fungivores. Genomic studies suggest that gene clustering in fungal metabolic pathways may be driven by the need to mitigate the accumulation of toxic intermediates, not necessarily by selection for consumer deterrence (McGary et al 2013). Additionally, the diversity and potency of mycotoxins can be influenced by environmental factors and metabolic constraints, complicating the interpretation of their ecological function (Awuchi et al 2022; Costantini et al 2024).

A Case Study: Psychoactive Mushrooms. Psychoactive compounds such as psilocybin, while not typically lethal, can impair locomotion or neural function in animal consumers, potentially increasing their predation risk and thus aiding spore dispersal. This supports the hypothesis that even non-lethal toxins can provide selective advantages to fungi by influencing consumer behavior and facilitating reproductive success (Awuchi et al 2022).

Conclusions. The evolution of fungal toxicity appears to be, at least in part, an adaptive response to selective pressures imposed by fungivory, particularly from invertebrates and possibly from small vertebrate consumers. While there is strong theoretical support for the role of toxic secondary metabolites in deterring consumption, empirical evidence for reciprocal coevolution, whereby consumer species evolve resistance or behavioral avoidance in response, is limited and largely indirect. Available data suggest that animal consumers often rely on learned avoidance or social transmission of foraging strategies, rather than on fixed, genetically encoded resistance mechanisms. Moreover, the possibility that certain toxins, such as psychoactive compounds, function not to kill but to impair consumers in ways that benefit fungal fitness (e.g., enhancing spore dispersal) expands our understanding of chemical defense beyond lethality. Although conceptual models derived from plant–herbivore systems offer valuable analogies, fungal–consumer interactions remain comparatively understudied, and further research is needed to clarify the evolutionary dynamics at play. Ultimately, the coevolution of fungal toxicity and consumer behavior likely encompasses a spectrum of defensive strategies, ranging from generalist deterrence to specialized toxin–consumer interactions, embedded within broader ecological and phylogenetic contexts.

Conflict of Interest. The authors declare that there is no conflict of interest.

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