

Review Article

Specialized Fungal Parasites and Opportunistic Fungi in Gardens of Attine Ants

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Ants in the tribe Attini (Hymenoptera: Formicidae) comprise about 230 described species that share the same characteristic: all coevolved in an ancient mutualism with basidiomycetous fungi cultivated for food. In this paper we focused on fungi other than the mutualistic cultivar and their roles in the attine ant symbiosis. Specialized fungal parasites in the genus *Escovopsis* negatively impact the fungus gardens. Many fungal parasites may have small impacts on the ants' fungal colony when the colony is balanced, but then may opportunistically shift to having large impacts if the ants' colony becomes unbalanced.

1. Introduction

Restricted to the New World, the approximately 230 fungus-growing ant species in the tribe Attini cultivate basidiomycetous fungi on freshly harvested plant substrate [1–3]. A well-known subset of species in this tribe, the leaf-cutting ants, are considered the most important herbivores in the Neotropics [4, 5], due to the large amount of fresh leaves and flower parts that workers cut and use to nourish the mutualistic fungal cultivar.

The attine ant-fungal symbiosis is ancient and probably originated from ancestral ants occurring in the Amazon basin about 50 million years ago [6, 7]. Since then, the tribe Attini evolved five patterns of fungiculture that are currently recognized [6]. Thus, the lower and higher attine ant genera practice different types of fungiculture, which are classified according to the type of fungus and the type of substrates used to maintain the fungal partner [6]. Therefore, the various fungiculture can be defined as (i) lower attine agriculture performed by phylogenetically basal ant genera such as *Cyphomyrmex*, *Mycetagroicus*, and *Mycetophylax* which cultivate fungi in the tribe Leucocopriini [8, 9], (ii) a specific type of agriculture performed by some species of the lower attine genus *Apterostigma*, which cultivates fungi within the

family Pterulaceae (the “coral fungi” [10, 11]), (iii) a group of ants that cultivate Leucocopriini fungi in the yeast form (ants in the *Cyphomyrmex rimosus* group), (iv) the higher attine agriculture that encompass the derived genera *Trachymyrmex* and *Sericomyrmex* which cultivate phylogenetically derived fungi within the Leucocopriini, mostly on fallen vegetation or organic matter, and finally (v) a specific group of ants within the higher agriculture, the leaf-cutting ants, cultivate a recent clade of derived Leucocopriini fungi [12].

Evidence shows that attine ants domesticated their fungal cultivars during the evolution of the symbiosis [8]. Thus, the evolutionary history of fungus-growing ants was marked by several horizontal transfers (switches) of cultivars. Particularly, within the lower attine fungiculture these cultivar switches occurred multiple times [8]. Mikheyev et al. [13] demonstrated that leaf-cutting ants cultivate the same species of cultivar, *Leucoagaricus gongylophorus* in an association known as “many to one.” Interestingly, it was found that in colonies of leaf-cutting ant, just a single clone of the mutualistic fungus is cultivated by workers [14, 15].

Since the detailed study by Möller [16], it is known that attine fungiculture is continuously exposed to alien microorganisms. As fungus-growing ants rely on the mutualistic fungi as the main food source for the colony, fungiculture

requires from workers several mechanisms to keep their cultivars protected from alien microorganisms that would harm the symbiosis [17].

The most important strategies applied by attine ants in order to preserve their nests from harmful microbes consist of mechanical and chemical barriers including (i) careful cleaning of the leaf fragments used as substrate for the fungal cultivar in order to put away spores and microorganisms [18, 19]; (ii) massive inoculation of the mutualistic fungus mycelium onto the clean plant fragment increasing the colonization of this substrate by the cultivar [2]; (iii) the use of antimicrobial glandular secretions [20–24] and faecal droplets [25, 26]; (iv) weeding and grooming of infected parts of the garden when an undesired microorganism is detected [18]; (v) antagonistic activity of the mutualistic fungus against alien microorganisms [14, 19]; (vi) unspecific microbial interrelationship between microorganisms which benefit the whole nest [26]; (vii) control of humidity in disposal chambers [27]; (viii) association with antibiotic-producing bacteria [28–36]. Despite such mechanisms to suppress the development of alien microbes, a plethora of bacteria, filamentous fungi and yeasts are still found in ant gardens [35, 37–41].

Fungi on the genus *Escovopsis* are considered specialized parasites of attine gardens while others are consistently isolated in association with attine gardens and need further studies to understand their role as symbionts. Here, we focus on *Escovopsis* sp. and the additional filamentous fungi and yeasts found in attine gardens and address the few studies that have explored the role of such microorganisms in the attine ant-fungal symbiosis.

2. *Escovopsis* sp.: The Specialized Garden Parasite of Fungus-Growing Ants

The existence of the anamorphic fungus of the genus *Escovopsis* (Figure 1) was observed by various researchers [2, 42] and was uniquely discussed for the first time by Möller [16]. Recently, Currie et al. [37] reported that *Escovopsis* sp. is associated with several genera of attine ants and is considered a parasite of the fungus cultivated by these insects [43]. Except for fungus-growing ants in the *Cyphomyrmex rimosus* group, this parasite has been found in most attine ant genera with frequency of occurrence ranging from 11% to 75% [37, 38, 44, 45].

Escovopsis sp. can affect fungus gardens in various manners: in extreme cases, the parasite grows rapidly over the colony, resulting into its total collapse [45] (Figure 2). According to experiments conducted by Currie [45], *Escovopsis* can remain in the colony for an extended period of time, thereby, suppressing subsequent colony development. Such impacts on the ant colony are supposed to be due to the necrotrophic action of *Escovopsis* sp. towards the cultivar [43].

With respect to the occurrence of *Escovopsis*, so far, this parasite was not recorded from any other environmental source other than in association with attine ants, a pointer to a long history of coevolution with these ants and their

mutualistic fungi [46]. This ancient evolutionary pattern resulted in broad phylogenetic associations between the various types of fungiculture and specific phylogenetic lineages of *Escovopsis* [46–49] as it is the case of the relationship of this mycoparasite and ants in the genus *Apterostigma* that are naturally threatened by a specific lineage of *Escovopsis* sp. [44]. This lineage comprises four *Escovopsis* morphotypes defined on the basis of conidial colours ranging between white, yellow, pink, or brown [44].

Meanwhile, within a particular fungiculture group, the same *Escovopsis* sp. strain can be associated with many genera of ants and vice versa, demonstrating that the interrelationship is apparently nonspecific or weak at a finer phylogenetic level [50, 51]. Even in the same nest, different *Escovopsis* strains can be found as confirmed in the work of Taerum et al. [52], who verified that 67% of the colonies of *Atta* sp. and *Acromyrmex* sp. were infected by multiple strains of the parasite. Interestingly, such strains did not engage in interference competition for their hosts [52].

So far, only two species are formally recognized in this genus, namely, *Escovopsis weberi* [53] and *Escovopsis aspergilloides* [54]. These species were originally isolated from gardens of *Atta* sp. (in Brazil) and *Trachymyrmex ruthae* (in Trinidad and Tobago), respectively. Available data indicate that there exists a high variation in the morphology and genetic characteristics among strains of the two currently known *Escovopsis* species [44], suggesting that putative new species in this genus may be described in the near future [44, 55].

Several aspects of the biology of *Escovopsis* sp. still remain undiscovered. Nothing is known about their life cycle or whether there is a teleomorphic (sexual) state. Also, the mode of transmission between colonies is unknown. Regarding this aspect, Currie et al. [37] suggest that transmission may be through other arthropods that visit or inhabit the nests, such as mites. As a matter of fact, vertical transmission (from parental to offspring colonies) of this fungus has not been observed.

Considering the harmful effect and close relationship with the attine cultivar [49], it is not surprising to consider that this parasite could be used as a biocontrol agent. Accordingly, Folgarait et al. [56] studied the antagonistic effect of *Escovopsis* sp. towards three strains of the mutualistic fungus. The authors' findings indicate that, under *in vitro* conditions, *Escovopsis* sp. retarded the growth of the mutualistic fungus of *Acromyrmex lundii* and this effect is *Escovopsis* strain dependent. Similar results were previously reported by Silva et al. [57] in *in vitro* bioassays using one *Escovopsis* sp. strain and the mutualistic fungus of *A. sexdens rubropilosa*.

Despite these preliminary results about *Escovopsis* sp. as a potential agent of biological control, the ants' defensive mechanisms need to be considered. As a result of *Escovopsis* sp. infection ant colonies first mount a generalized response through a large mobilization of the individuals [58]. Second, workers physically remove and concentrate spores in the infrabuccal cavity [18, 59] (grooming); in addition, workers remove affected parts of the fungus gardens [18] (weeding). Regarding these two ant behaviours, there seems to exist caste specialization [60] and recruitment of workers to the site

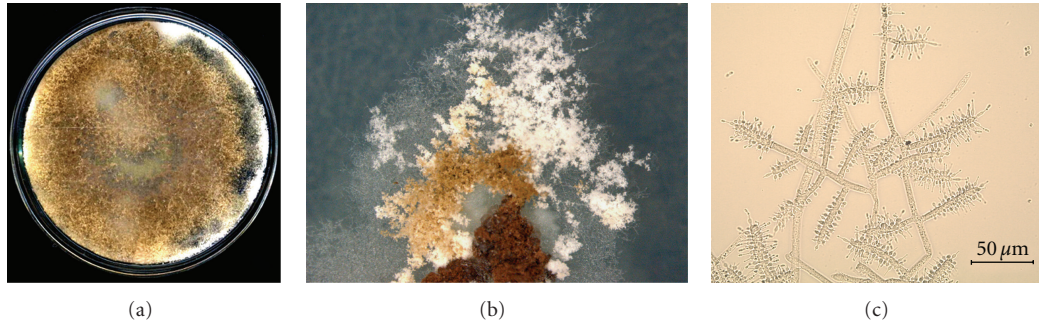


FIGURE 1: *Escovopsis* sp. parasites from fungus-growing ants. (a) General aspect of *Escovopsis* sp. isolated from the leaf-cutting ant *Atta sexdens rubropilosa* (Corumbataí, Brazil) cultured in potato dextrose agar (PDA) for 6 days at 25°C. (b) Close view of *Escovopsis* sp. isolated from *Acromyrmex lobicornis* (Santa Fé, Argentina) in PDA after 5 days at 25°C. (c) *Escovopsis* sp. conidiophores from (a). Note the cylindrical vesicles covered with ampulliform phialides.

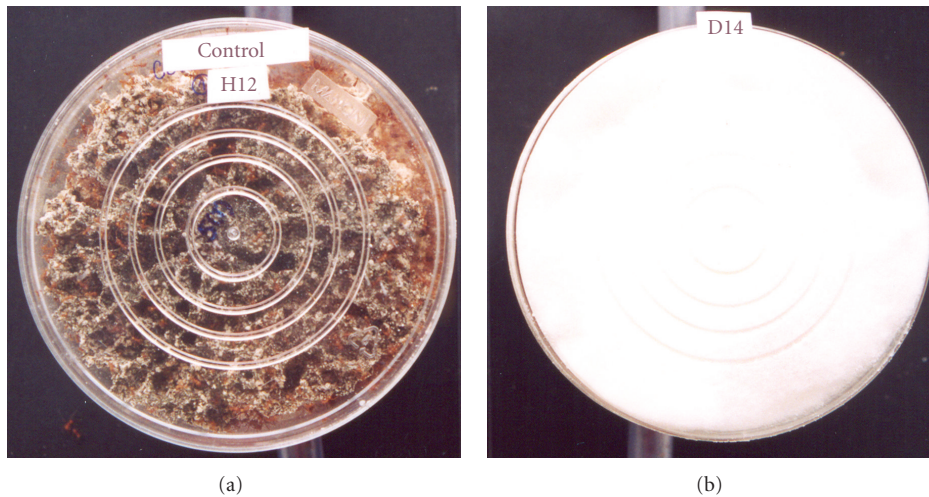


FIGURE 2: Laboratory colonies of *Atta sexdens rubropilosa* (Corumbataí, Brazil). Colonies were treated with baits without insecticide, control (a) and formulated baits containing the insecticide Hydramethylnon (b). *Escovopsis* sp. (white mycelia) emerged two days after treatment from fungus gardens of the infected colony (b), which depicts the aggressive effect of such parasite on attine ant colonies.

of infection [61]. An additional important factor that may impair the use of *Escovopsis* as agent of biological control is their low spore viability (about 3% viability [24]) and it should be considered on the development of biological control methods.

Perhaps the most effective defensive mechanism against *Escovopsis* sp. is the association of attine ants with microbial symbionts capable of producing antifungal substances. For example, ants are associated with *Pseudonocardia*, a group of bacteria found in the ant's exoskeleton that antagonize *Escovopsis* sp. and which is vertically transmitted during the foundation of new nests [28, 62]. Additionally, other microorganisms may antagonize *Escovopsis* sp. such as *Amycolatopsis* sp. [35], *Burkholderia* sp. [63], *Streptomyces* [32, 34, 35, 64], and yeasts [65]. Thus, rather than a one-to-one symbiosis between the ants and their fungi, recent work suggests that rather the ants rely on a consortium of microbes and their compounds to defend themselves against *Escovopsis* sp. parasites [26].

3. Occurrence of Additional Fungi on Gardens of Attine Ants and Their Possible Role as Symbionts

Evolutionary theory predicts that organisms with restricted genetic diversity are susceptible to exploitation by several parasites [66]. This can be the case of attine ants which cultivate a single strain of the mutualistic fungus [14, 15]. Since the fungus garden is an ideal environment for the growth of the fungal cultivar, it is expected that additional alien fungi would exploit this substrate.

As indicated earlier, Möller [16] was the first to record the existence of filamentous fungi in attine gardens. In addition to the fungus that was later named *Escovopsis* sp. and to which the author referred as the "strong state" of the mutualist cultivar, Möller [16] provided detailed information on the occurrence of *Aspergillus* sp., *Mucor* sp., *Penicillium*, and *Rhizopus* sp. on the fungus gardens of *Acromyrmex disciger* (collected in Blumenau, Brazil). This author reported

that such filamentous fungi covered the fungus gardens when left unattended by workers. Later, Spegazzini [67] found ascocarps of *Xylaria micrura* in abandoned nests of *Acromyrmex lundii* in Argentina and also provided detailed drawings of this structure. When working with laboratory nests of *Trachymyrmex septentrionalis*, Weber [68] observed that gardens were also overgrown by several filamentous fungi such as *Aspergillus* sp., *Mucor* sp., and *Penicillium* sp. Kreisel [42] also observed *Cunninghamella* sp., *Fusarium* sp., *Rhizopus* sp., and *Trichoderma* sp. when studying fungus gardens of *Atta insularis* (in Cuba) unattended by workers. Similarly, Bass and Cherrett [69] studying the roles that workers play on the fungus garden maintenance observed that *Aspergillus* sp., *Cladosporium* sp., *Fusarium* sp., *Mucor* sp. and *Penicillium* sp. quickly overgrow gardens when left unattended by workers for several days. Luciano et al. [70] found *Aspergillus* sp., *Nigrospora* sp., and *Penicillium* sp. growing on the fungus garden of laboratory colonies of *Acromyrmex heyeri* in south Brazil.

Fisher et al. [39] demonstrated that *Atta cephalotes* colonies reared in the laboratory presented a shift in the fungal species composition when offered different plant substrates, thus providing the first experimental evidence that the fungal community on attine gardens may be influenced by the type of plant substrate used in the experiments. In addition, Currie et al. [37] demonstrated that gardens from diverse attine ant genera spanning all the phylogenetic diversity of the tribe Attini harbor alien fungi. These authors studied mostly attine ants from Central America and particular attention was drawn to the garden parasite *Escovopsis* sp. but several other fungi also occurred which were not identified [37]. Following this study, Ortiz et al. [71] reported the occurrence of *Fusarium* sp., *Rhizopus* sp., and *Trichoderma lignorum* when studying fungus garden fragments left unattended by workers of *A. cephalotes* (in Colombia). Barbosa et al. [72] and Barbosa [73] also reported a comprehensive list of species of filamentous fungi present in fungus gardens of *Atta laevigata* field nests in northeastern Brazil and concluded that the genus *Trichoderma* was prevalent in such gardens.

In addition to reports about filamentous fungi several authors also recorded a variety of yeasts on nests of attine ants. For example, Craven et al. [74] provided the first evidence that attine gardens contain yeasts using scanning electron microscopy. Pagnocca et al. [75] and Carreiro et al. [40] were the first to systematically study the yeast populations on laboratory colonies of *A. sexdens rubropilosa*. Such authors found variations in the abundance of yeasts populations in gardens and pointed out that *Candida*, *Cryptococcus*, *Pichia*, *Rhodotorula*, *Sporobolomyces*, *Tremella*, and *Trichosporon* were the prevalent genera. Carreiro et al. [76] showed that yeasts found on attine gardens produce the so-called killer toxins (or mycocins), which were proposed to be involved on the regulation of yeast populations on attine gardens. In this sense, Rodrigues et al. [65] proposed that yeasts may have a protective role in attine gardens against alien filamentous fungi. Up to date, the yeast survey on attine gardens rendered the description of three new species: *Cryptococcus haglerorum* [77], *Blastobotrys attinorum* (= *Sympodiomyces attinorum* [78]), and *Trichosporon*

chiarellii [79]; however, there is evidence that additional new yeast species associated with these insects await discovery. Recently, black yeasts in the genus *Phialophora* were reported to live on the exoskeleton of attine ants [80, 81] and the authors pointed out that they could antagonize the protective role of their symbiotic *Pseudonocardia*. Polysaccharidases secreted by yeasts and bacteria [82, 83] may also be important for the nest homeostasis and it is an open field for further investigation.

Despite the proposed roles that yeasts may play on attine gardens, few studies focused on the potential roles that filamentous fungi may perform on the attine ant-fungal interaction. Several filamentous fungi found in attine gardens are commonly found in soil or plant substrates, suggesting that these microorganisms are probably transported on the workers' integument or introduced into gardens via the plant material collected by the foraging workers [38, 41, 84]. Thus, it has been suggested that filamentous fungi are present in the fungus gardens as transient spores and may not play significant roles in the symbiosis [85]. In agreement with this hypothesis, Currie and Stuart [18] observed that when *Atta* sp. gardens are experimentally infected with *Trichoderma* sp. spores (a generalist fungus in comparison to *Escovopsis* sp.), the ants groom out spores efficiently that it is apparently removed from gardens. In contrast, gardens infected with *Escovopsis* sp. spores sustained long-term infections. Thus, this result suggests that general fungi like *Trichoderma* sp. may not play any role in the symbiosis [18].

On the other hand, recent studies address that filamentous fungi may play important roles in gardens of fungus-growing ants. Considering the studies reviewed here it is clear that a common trend arises: filamentous fungi (i) are found in association with diverse genera of attine ants, (ii) are found in attine nests from different localities, and, most important, (iii) quickly develop when the fungus gardens are unattended by workers (Figure 3).

In this sense, Rodrigues et al. [86] determined that the majority of microfungi found in gardens of *A. sexdens rubropilosa*, a leaf-cutting ant species spread all over Brazil, belong to genera commonly found in soil and plant substrate. Particularly, the fungus *Syncephalastrum racemosum* was found in 54% of gardens from laboratory nests treated with baits supplemented with the insecticide sulfluramid (commonly used in Brazil to control leaf-cutting ants). A variety of other fungi, including *Fusarium solani*, were found in such gardens but with fewer than 20% of prevalence. None of the laboratory nests used as control (either treated with *Eucalyptus* sp. leaves or baits without insecticide) had the fungus gardens overgrown by filamentous fungi. On the other hand, *Fusarium oxysporum* and *Trichoderma harzianum* were found in 23% and 38% of gardens from field nests treated with baits supplemented with sulfluramid, respectively. It is interesting to note that *S. racemosum* was not observed in gardens from nests treated with insecticides under field conditions [86]. In addition, *Escovopsis* sp. was isolated in 21% and 15% in gardens of laboratory and field nests treated with sulfluramid, respectively [86]. In another experiment, several microfungi species were observed to quickly overgrow the fungus garden of *A. sexdens rubropilosa*

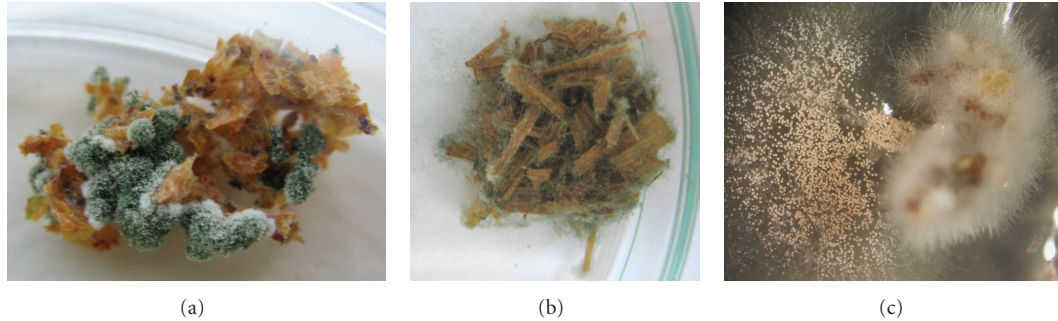


FIGURE 3: Fungus garden fragments of leaf-cutting ants overgrown by filamentous fungi. (a) *Atta texana* garden fragment (TX, USA) with green tufts of *Trichoderma* sp. (b) *Atta bisphaerica* garden fragment (Botucatu, Brazil) with green conidiation of *Trichoderma* sp. Workers from (a) and (b) were manually removed and garden fragments were kept in wet chambers for 5 days at 25° C. (c) Isolation plate showing fungus garden fragment on potato dextrose agar medium supplemented with 150 $\mu\text{g}\cdot\text{mL}^{-1}$ of chloramphenicol. On the right note the white mycelia of the mutualistic fungus of attine ants and on the left the microfungus *Aspergillus* sp. Both fungi emerged from the garden fragment.

($n = 12$) when workers were experimentally removed [87]. The observed species included *Acremonium kiliense* (42%), *E. weberi* (42%), *Trichoderma* sp. (50%), and a fungus previously identified as *Moniliella suaveolens* (50%), which now is known to be a genus not yet described (Harry Evans, personal communication). Similarly, Carlos et al. [88] found several fungal species including *Penicillium* spp. and *S. racemosum* on *A. sexdens rubropilosa* gardens when treated with a variety of formulated insecticides.

In another systematic study, filamentous fungi were also reported from field nests of several species of *Acromyrmex* from south Brazil [38]. The authors observed a high diversity of fungi and noted that *F. oxysporum*, *Escovopsis* sp., and *Cunninghamella binariae* were present in 40.5%, 27%, and 19%, respectively, out of 37 nests. In contrast with previous studies, *S. racemosum* was found in 5.4% of the nests. Recently, Rodrigues et al. [41] showed that *Cyphomyrmex wheeleri* ($n = 16$ nests), *Trachymyrmex septentrionalis* ($n = 16$), and *Atta texana* ($n = 4$) sampled in Texas (USA) harbor a diverse community of microfungi which varies across seasons and are structured, in part, by location where nests were collected, reflecting a spatial component on the structuring of fungal communities. Interestingly, both *Escovopsis* sp. and *S. racemosum* were not found in the studied nests.

Moreover, many filamentous fungi are carried by the female alates (gynes) of leaf-cutting ants during the foundation of a new nest [89–91]. These microorganisms were more prevalent on the integument than in pellets found in the infrabuccal pocket [37, 91]. Although such fungi may be accidentally transported by gynes, they compose the initial microbiota associated with the ant nests and might be involved in the success on the establishment of a new nest. In fact, Autuori [92, 93] reported that several incipient nests do not thrive the period following the nuptial flight. In addition to flooding and birds, this author argued that fungi were also responsible for the mortality of incipient nests [93].

An additional observation sheds light on the possible role of filamentous fungi as opportunistic antagonists. When laboratory subcolonies of *A. sexdens rubropilosa* were artificially infected with spores suspensions of *Fusarium solani*, *Trichoderma* cf. *harzianum*, *S. racemosum*, and *E.*

weberi, Rodrigues et al. [94] observed that only nests treated with *E. weberi* provided a persistent infection (detected up to 300 hours after infection). However, about twelve hours after treatment with *S. racemosum* spores, workers removed fragments of fungus gardens and dumped away from gardens. This observation parallels the weeding behavior originally described as a specific adaptation for removing germinated spores of *Escovopsis* sp. [18]. Dumped fragments were collected and after plating quickly revealed the presence of *S. racemosum* [94].

In addition to *Escovopsis* sp. other filamentous fungi were thought to be used as biological control agents [95]. Thus, attempts to use fungal spores on bait formulations demonstrated the effectiveness of this approach. Formulated baits with a combination of spores of *Metarhizium anisopliae* (an insect pathogenic fungi) and *Trichoderma viride* (opportunistic antagonist of the ant cultivar) controlled 100% of laboratory colonies of *Atta cephalotes* compared to the control (nests treated with baits without spores) [95]. Field experiments showed that baits with *M. anisopliae* and *T. viride* spores achieved 100% of nest mortality when compared to the insecticide Pirimiphos-methyl, which caused 60% of nest mortality. However, the time necessary to achieve 100% of nest mortality using the formulated baits was more than 60 days [95], which is considered ineffective for controlling leaf-cutting ants in large areas. Despite the failure of such attempts these initiatives are desirable and perhaps will guide the development of alternative techniques to control these pest ants.

4. Conclusions and Future Directions

The evidence gathered so far suggests that filamentous fungi act as opportunistic antagonists on the attine ant-fungal interaction. In comparison to the specialized fungus *Escovopsis* sp., filamentous fungi are considered nonspecific antagonists of the ant cultivar. The antagonistic effect of these fungi is evident in disturbed gardens (either caused by insecticides or other unknown factor), when gardens are unattended by workers and on incipient nests. Future

experimental studies should systematically address whether filamentous fungi also influence healthy colonies. The results of such studies will ultimately help in the development of new strategies for controlling leaf-cutting ants.

Finally, despite the arguments in favour of the antagonistic nature of filamentous fungi, we do not rule out that some may have other unknown functions in the attine ant symbiosis. For instance, Freinkman et al. [96] demonstrated that fungi may be a potential source of new compounds as it is the case of bionectriol A, isolated from *Bionectria* sp. derived from the fungus gardens of *Apterostigma dentigerum*. Perhaps, future reports will unravel the existence of filamentous fungi that are beneficial to the ant colony. This aspect is totally unexplored and should also be considered when studying such microorganisms.

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