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ARTICLE
Microbial Ecology

Tri-trophic interactions of soil mite *Sancassania polyphyllae* (Acari: Acaridae) with fungal biocontrol agents

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Abstract

Mycophagous invertebrates can significantly impact the efficacy of fungal biocontrol agents; yet the interaction between these agents and *Sancassania polyphyllae* (Acari: Acaridae), commonly found in soil ecosystems, remains poorly understood. Our study demonstrates that *Sa. polyphyllae* mites feed on fungus-infected insect cadavers as well as the mycelium and spores of *Trichoderma afroharzianum* and *Metarhizium brunneum* in pure cultures. Mite feeding activity was greater on *Trichoderma* than *Metarhizium* pure cultures, possibly due to *Metarhizium*'s acaricidal effects, which impacted mite activity. Furthermore, mite feeding on fungus-infected insect cadavers caused visible damage to the integument. This feeding behavior significantly impacted fungal sporulation, a key factor in biocontrol efficacy. In both the *M. brunneum*-infected *Galleria* groups and the *Tr. afroharzianum*-infected *Galleria* groups, mite numbers increased over time, peaking around 9–11 days post-infection before slightly declining or plateauing. Notably, the fungi-infected insect tissue consistently exhibited significantly higher mite numbers than the pure cultures group at several time points. In dual-culture assays, *Sa. polyphyllae* mites preferentially fed on *Fusarium oxysporum* over *Tr. afroharzianum*. The presence of *Fusarium* may influence mite behavior and potentially reduce their impact on *Trichoderma*. This preference, possibly nutritional, requires further investigation. Consequently, *Trichoderma*'s suppression of *Fusarium* in soil could significantly impact the food resources available to soil-dwelling mites like *Sa. polyphyllae*. Further research is needed to determine the nutritional basis of this feeding preference.

KEYWORDS
Astigmata, biological control, entomopathogenic fungi, infection, mycoparasitic fungi, *Sancassania*

INTRODUCTION

Interspecific competition is a fundamental ecological force shaping terrestrial life through diverse interactions among organisms and their abiotic environment (Bedau, 2005; Hibbing et al., 2010). Within the soil biome, *Trichoderma* and *Metarhizium* are cosmopolitan fungi frequently employed in agricultural biocontrol, but

their distinct modes of action lead to different effects on soil communities. *Metarhizium* is primarily an entomopathogenic agent, capable of infecting a wide range of arthropods, including ticks, mites, and insects (Dogan et al., 2017; Samish et al., 2014; St. Leger & Wang, 2020). Notably, *Metarhizium* species effectively control recalcitrant coleopteran pests, including *Oryctes* spp., significant threats to palms (Prastowo et al., 2022) and various white grubs (*Melolontha* spp., *Holotrichia serrata*, *Pentodon algerinum*), which damage crops such as sugarcane, strawberries, and turfgrass by feeding on roots, hindering nutrient and water uptake (Malusá et al., 2020; Ramanujam et al., 2021; Zimmermann, 2007). Conversely, *Trichoderma* exhibits a primary antagonistic effect on fungal communities, effectively reducing fungal populations through mycoparasitism and competition (Yao et al., 2023). Many *Trichoderma* strains effectively control a range of plant fungal pathogens including *Botrytis*, *Sclerotium*, *Alternaria*, *Fusarium*, *Pythium*, and *Rhizoctonia* (Marraschi et al., 2019; Tyśkiewicz et al., 2022), and certain *Trichoderma* strains have demonstrated entomopathogenic effects against various insects (Anwar et al., 2016; Nasution et al., 2018) and phytophagous mite pests (Evren et al., 2025).

As rhizosphere colonizers and endophytes, both fungal genera exhibit plant-growth-promoting properties by enhancing nutrient uptake, triggering induced systemic resistance, and increasing plant resilience to biotic and abiotic stress (Tseng et al., 2020; Wood et al., 2022). These fungi represent valuable tools in biological control strategies and as such, their use has increased in recent years, offering new alternatives to chemical pesticides (Lacey et al., 2015; Stone & Bidochka, 2020). Applied to both the phyllosphere and rhizosphere, these fungal biocontrol agents can infect and influence the behavior of arthropods inhabiting those environments (Bruck, 2010; Hussien et al., 2025). Studies examining the interactions between these fungi, especially *Metarhizium*, and nontarget arthropods (e.g., ants, syrphids, lacewings, and coccinellids) suggest that while contact infection can occur, overall effects on these groups appear negligible (Abonyo et al., 2016; Corallo et al., 2021; de Azevedo et al., 2017; Dogan et al., 2017; Novgorodova et al., 2022; Traugott et al., 2005). Furthermore, several microarthropod groups have been reported to carry spores of EPF in soil (Schabel, 1982); however, some nontargets avoid *Metarhizium*-treated areas or present feeding avoidance behavior toward fungi-infected cadavers (Bayissa et al., 2016; Meyling & Pell, 2006). Research into the nontarget effects of *Trichoderma* remains limited. Existing evidence suggests that *Trichoderma* application can influence the behavior and feeding habits of nontarget organisms. For instance, a termite species *Odontotermes formosanus* (Fam: Termitidae) has been observed to avoid tunneling in areas treated with *Trichoderma* spores (Xiong et al., 2018), while bean weevil *Acanthoscelides obtectus* (Fam: Chrysomelidae) exhibited a 10% reduction in feeding on treated bean seeds, indicating a potential repellent effect (Rodríguez-González et al., 2020). It is worth acknowledging the possibility that they might impact other beneficial groups, particularly mite populations (Touray, Ulug, et al., 2025).

Soil mites are essential to soil ecosystems. Various taxa contribute to nutrient cycling and serve as indicators of soil health due to their sensitivity to environmental changes (De Groot et al., 2016; Huguier et al., 2015). *Sancassania polyphyllae* (Acari: Acaridae) are ubiquitous, free-living mites inhabiting diverse environments, including soil and aquatic habitats. These mites maintain symbiotic relationships with various arthropods, notably scarabaeid beetles (Al-Deeb et al., 2012; Cakmak et al., 2010, 2011; Estrada-Bárcenas et al., 2010; Krantz et al., 2009). Exhibiting phoretic, saprophagous, or necrophagous behavior, they attach to hosts. Following the death of their carrier, mites feed on the phoretic host and subsequently reproduce rapidly. They also consume organic matter and fungi (Al-Deeb et al., 2012; Cakmak et al., 2011; Houck & OConnor, 1991; Krantz et al., 2009). Notably, *Sancassania* mites have been recognized as beneficial acarids with a potential role in plant-parasitic nematode population regulation, and are integral components of this complex soil ecosystem (Sell, 1988). However, their presence can influence the role of biocontrol agents like soil-dwelling entomopathogenic nematodes, insect pathogens used for the control of soil-dwelling pests. *Sa. polyphyllae* has been demonstrated to consume the infective juvenile stage of *Steinernema feltiae* and *Heterorhabditis bacteriophora* (Fam: Steinernematidae, Heterorhabditidae) as well as nematode-infected cadavers (Cakmak et al., 2010, 2013; Karagoz et al., 2007).

Despite the established success of entomopathogens against white grubs (Koppenhöfer & Fuzy, 2003; Li et al., 2023; Malusá et al., 2020; Ramanujam et al., 2021), and the increasing use of *Trichoderma* and *Metarhizium* in biocontrol, the potential effects on phoretic astigmatid mites and nontarget mites like *Sa. polyphyllae* require further investigation. We hypothesize that *Metarhizium* and *Trichoderma* may exhibit toxicity or induce avoidance behavior in *Sa. polyphyllae*, affecting their population dynamics. Conversely, we hypothesize that these mites will reduce the efficacy of *Metarhizium* and *Trichoderma* as biocontrol agents by consuming fungal propagules (e.g., spores, conidia, and hyphae) or fungi-infected cadavers, leading to a measurable decrease in fungal colony size/density and a subsequent reduction in their impact on target pests.

MATERIALS AND METHODS

Mite, fungal, and insect maintenance

Mites were obtained from dead scarab larvae collected from a strawberry field in Sultanhisar, Aydin. They were identified as *Sa. polyphyllae* using chaetotaxy and further validated by comparison with reference specimens from prior studies (Ekmen, Cakmak, et al., 2010; Ekmen, Hazir, et al., 2010). Cultures were maintained in the laboratory at 24°C on freeze-killed *Galleria mellonella* (Lepidoptera: Pyralidae) and *Tenebrio molitor* (Coleoptera: Tenebrionidae) larvae.

Galleria mellonella cultures were maintained in a controlled insectary with a temperature of 28°C. Larvae were fed on an artificial diet consisting of corn flour, wheat flour, powdered milk, honey, glycerine, beeswax, and yeast. Fourth-stage larvae were submerged in water at 60°C for 5 s; this heat treatment prevents cocoon production (Hazir et al., 2022). *Tenebrio molitor* was reared on potatoes, corn flour, and wheat flour.

Trichoderma afroharzianum (strain Tr95), *Metarhizium brunneum* (Met52), and *Fusarium oxysporum* were used in this study. *Tr. afroharzianum* was isolated from a strawberry field in Incirliova, Aydin (Korkom, 2022). Fungi were maintained on potato dextrose agar (PDA) (Merck, Darmstadt-Germany) at 25°C in darkness.

Acaricidal effects of fungi

To determine if *Tr. afroharzianum* and *M. brunneum* spores infect *Sa. polyphyllae* mites, *Galleria* larvae were treated with fungal spores. Briefly, to obtain fungal spores, fungal cultures were flooded with sterile 0.01% Tween 80 water and the surface was gently scraped. The obtained suspension was filtered using sterile gauze to remove mycelial fragments. The spore concentration was adjusted to 1×10^7 conidia/mL, and 20 μL of spore suspension was inoculated on PDA to ensure that spore viability was >90% (Köhl et al., 2024). Freeze-killed *G. mellonella* larvae were placed on water agar in 9-cm Petri dishes. One milliliter of fungal spores was sprayed on insect cadavers and surrounding agar medium. After an hour, 10 female mites were placed on treated insects. Petri dishes were sealed with parafilm. Mite mortality was assessed for 7 days post-treatment. To verify death, mites were carefully probed with a fine brush, and those exhibiting no movement were recorded as deceased. Each treatment had five replicates and the experiment was conducted twice.

Mycophagous activity of *Sa. polyphyllae*

Pure fungal cultures

After investigating the effect of *Tr. afroharzianum* and *M. brunneum* on *Sa. polyphyllae* survival, this experiment aimed to investigate the mycophagous activity of *Sa. polyphyllae* and to determine if these mites can survive and reproduce on *Tr. afroharzianum* and *M. brunneum* alone. Fungi were cultured individually on 9-cm PDA plates using mycelial plugs from pure cultures and allowed to establish for four days. Subsequently, three live mites (two females and one male) were introduced using a fine brush to each Petri dish containing the established fungal cultures of either *Trichoderma* or *Metarhizium*. Control groups included plates with no mites to compare fungal growth in the absence of *Sa. polyphyllae*. The population of mites and fungal growth were monitored over 2 weeks by recording the number of individuals in each plate every three days (Estrada-Bárcenas et al., 2010). Each treatment had at least four replicates in each experiment and was repeated once.

Fungi-infected insect cadavers

G. mellonella larvae were infected with fungi spores that were obtained from sporulating cultures. Fungal spores were prepared as mentioned above. Insect larvae were treated with 1 mL of spore suspension (1×10^7 spores/mL) in Petri dishes lined with filter paper. The plates were kept at 24°C in the dark until death. Afterwards, *Trichoderma* and *Metarhizium*-infected *G. mellonella* cadaver (5 days post death) or freeze-killed cadavers were placed on water agar (agar 1% w/v, Condolab, Madrid-Spain) in Petri dishes (6 cm). Each Petri dish had one insect larva. Subsequently, three live mites (two females and one male) were introduced using a fine brush on each larva. The feeding effects of *Sa. polyphyllae* mites on insect cadavers and the population of mites were monitored over 18 days by recording the number of individuals in each plate. Each treatment had at least five replicates and was repeated once.

Interactions between *Trichoderma*, *Fusarium*, and *Sancassania*

This experiment investigates how *Sa. polyphyllae* mites influence the biocontrol efficacy of *Tr. afroharzianum* against *Fu. oxysporum*, focusing on three-way interactions. Simultaneously, *Trichoderma* and *Fusarium*

mycelial plugs, taken from 7-day-old pure cultures, were plated at opposite ends of the same PDA medium in Petri dishes (9 cm) to allow interaction. After 24 h, 10 adult *Sa. polyphyllae* mites (6 females, 4 males) were then introduced to the center of plates using a fine brush to plates containing both *Tr. afroharzianum* and *Fu. oxysporum*. Mite behavior, feeding preferences, and the impact on fungal growth were monitored. Control plates consisted of *Tr. afroharzianum* alone, *Fu. oxysporum* alone, and a combination of *Tr. afroharzianum* and *Fu. oxysporum* as shown below: (1) *Trichoderma* only (T); (2) *Fusarium* only (F); (3) *Trichoderma* + *Fusarium* (TF); (4) *Trichoderma* + *Sancassania* (TS); (5) *Fusarium* + *Sancassania* (FS); (6) *Trichoderma* + *Fusarium* + *Sancassania* (TFS).

All plates were incubated at 25°C in darkness. Colony radial growth of *Tr. afrohazianum* was measured at 3, 5, 7, 11, and 14 days post-infection. Antagonism against *Fu. oxysporum* was assessed visually using a scoring system (1, antagonist grows over the entire Petri dish; 2, antagonist grows over 3/4 of the plate; 3, antagonist and pathogen grow to half of the plate; 4, pathogen grows over 3/4 of the plate; and 5, pathogen grows throughout the Petri dish) (Otoya-Martinez et al., 2023). Sporulation of *Trichoderma* was assessed visually using a scoring system (1, very low sporulation, white or cream coloration, sparse mycelial growth; 2, low sporulation, little whitish-green coloration, appearing in some areas, moderate mycelial growth; 3, moderate sporulation, white-green coloration, dense growth with some aerial mycelium; and 4, high sporulation, grayish-green coloration typical of *Tr. afroharzianum*, dense mycelial growth). Each treatment had three replicates, and the experiments were repeated twice.

Choice assay

Trichoderma afroharzianum and *M. brunneum* conidia were obtained from sporulating cultures as described previously. Ten *G. mellonella* were infected with each fungus in Petri dishes (9 cm) and incubated at 25°C in darkness until death (within 7 days post-infection). In the choice experiments, two insect cadavers (one fungi-infected and one freeze-killed) were placed 7 cm apart on water agar in 9-cm Petri dishes and 10 *Sa. polyphyllae* mites (six females, four males) were placed in the center. The control consisted of two freeze-killed larvae. The Petri dishes were incubated at 25°C in darkness. The number of individual mites (adults and mobile developmental stages) on each cadaver was counted after 5 days. Each treatment had at least four replicates and the experiment was repeated twice. For the control, two freeze-killed larvae were placed in each Petri dish.

Statistical analysis

Data on mite mortality after exposure to fungal spores were arcine-transformed and analyzed using one-way ANOVA. Repeated-measures ANOVA (based on GLM) was used to compare mite population and to analyze fungal colony diameter over 14 days in the same Petri dishes across treatments. Tukey's honestly significant difference (HSD) post- hoc test was used for pairwise comparisons. Data on *Trichoderma* antagonism from in vitro experiments were analyzed using nonparametric ANOVA with Dunn's multiple comparison test.

Mite preference was quantified by calculating the difference in the proportion of mites (adults and mobile developmental stages) observed on each of the two cadaver types offered. To assess whether mite choices differed significantly from a random 50:50 distribution, a replicated G-test of goodness of fit was performed. This analysis examined heterogeneity among replicates (GH) and the deviation of the pooled data from a chance distribution (GP). The total deviation (GT) was then compared to a χ^2 distribution to determine statistical significance.

Statistical analysis and data visualization were performed using GraphPad Prism (v9), Excel, SPSS Statistics v23.

RESULTS

Acaricidal effects of fungi

Both *Tr. afroharzianum* and *M. brunneum* treatments resulted in only 8 ± 6% mite mortality after 7 days, and mortality in the control group was 1 ± 3%. Although *Sa. polyphyllae* mites exhibited low susceptibility to fungal infection, there was a significant difference between fungal treatments and control ($F = 4.366$; df = 2, 29; $p = 0.023$).

Mycophagous activity of *Sa. polyphyllae*

Direct observation confirmed that *Sa. polyphyllae* mites fed on both the mycelium and spores of *Tr. afroharzianum* and *M. brunneum*. Mite feeding activity appeared greater on *Trichoderma* cultures compared to *Metarhizium* cultures in Petri dish assays (Figure 1A).

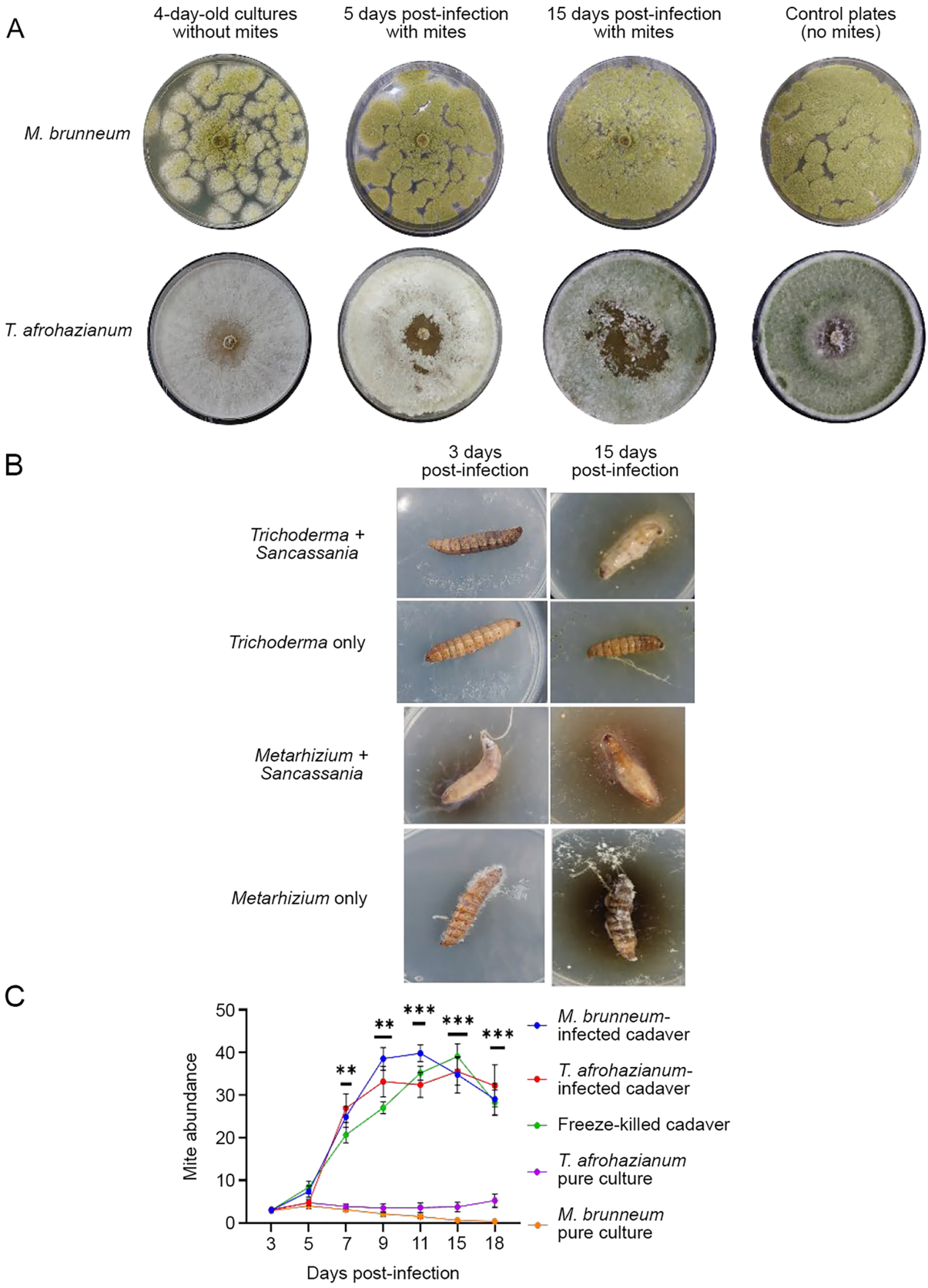

FIGURE 1 Legend on next page.

Both the *M. brunneum* and *Tr. afroharzianum* pure culture groups showed very low and relatively stable mite numbers over time. The mites could survive on the fungi; their numbers did not increase. Mites fed on fungi-infected *G. mellonella* cadavers. This feeding behavior damaged the integrity of the cadaver, resulting in visible damage to the cadaver integument, which greatly disrupts fungal development and fungal sporulation. This damage was more pronounced on cadavers infected with *M. brunneum* compared to those infected with *Tr. afroharzianum* (Figure 1B). Both the *M. brunneum* and *Tr. afroharzianum*-infected *Galleria* groups showed an increase in mite numbers over time, peaking around 9–11 days post-infection and then slightly declining or plateauing (Figure 1C). The *M. brunneum*-infected cadavers group showed significantly higher mite numbers compared to the *Tr. afroharzianum-infected* cadaver group at several time points. Repeated-measures ANOVA revealed significant effects of treatment ($F = 65.94$; df = 4, 210; $p < 0.0001$), time ($F = 119.6$; df = 6, 210; $p < 0.0001$), and their interaction ($F = 24.50$; df = 24, 210; $p < 0.0001$) on mite numbers. Post hoc analysis (Tukey's test) demonstrated that mite numbers on both fungi-infected and freeze-killed cadavers were significantly greater than on all pure fungal cultures at all time points after 5 days post-infection.

Interaction between *Trichoderma*, *Fusarium*, and *Sancassania*

Across all treatments, the mycelial growth rate of *Tr. afroharzianum* increased gradually post-inoculation, covering the entire Petri dish by 7 days post-infection (Table 1). There was no difference in the mycelial growth of *Trichoderma* in all the different groups ($p > 0.05$).

The presence of *Sa. polyphyllae* did not significantly inhibit *Tr. afroharzianum* growth in any treatment, but it did disrupt the growth pattern and had a slight negative effect on *Trichoderma* sporulation. In the *Trichoderma* only plates, fungal growth was uniform, dense, and circular, typical of *Trichoderma*. In the *Trichoderma* + *Fusarium* (TF) plates and in *Trichoderma* + *Fusarium* + *Sancassania* (TFS), *Trichoderma* exhibited complete antagonism against *Fusarium*. In the *Trichoderma* + *Sancassania* (TS) plates, *Trichoderma* growth was less uniform and dense compared to the *Trichoderma* only control. While there were distinct, separated colonies or patches in *Trichoderma* mycelial growth in the plates, *Fusarium* was completely suppressed. *Trichoderma* sporulation rate was negatively impacted by the presence of mites as compared to treatments without mites ($p < 0.0001$). Antagonistic effects were not affected by mites ($p > 0.05$) (Table 1, Figure 2).

Choice assay

This experiment examined mite preference between different types of insect cadavers. The number of individual mites (adults and mobile developmental stages) on each cadaver was counted after 5 days. The results showed no significant preference between freeze-killed cadavers in the control ($p = 0.84$) (Figure 3). The average mite count on freeze-killed cadavers was double that observed on *Trichoderma*-infected cadavers and *Metarhizium*-infected cadavers ($p < 0.01$), indicating that the mites significantly preferred freeze-killed cadavers over fungal-infected cadavers. In addition, even though the mites seemed to avoid both types of infected cadavers, mites significantly preferred *Trichoderma*-infected cadavers over *Metarhizium*-infected cadavers ($p < 0.001$).

DISCUSSION

Sancassania mites, along with fungal biocontrol agents from the genera *Metarhizium* and *Trichoderma*, occur naturally in soil ecosystems across many regions. This study investigated the bidirectional interactions between *Sa. polyphyllae* mites and these fungal biocontrol agents, a previously unexplored area. We examined how the presence of biocontrol fungi can impact mite populations, considering both the nutritional and pathogenic aspects of their relationship.

Our study demonstrated that *Sa. polyphyllae* mites fed on both the mycelium and spores of *Tr. afroharzianum* and *M. brunneum*, as well as on insect cadavers infected

FIGURE 1 (A) Macromorphological changes in fungi colonies infested with *Sancassania polyphyllae*. The mites were observed grazing on the fungal mycelia, leading to the patchy growth in the center of *Trichoderma afrohazianum* plates. (B) Macromorphological changes in fungi-infected *Galleria* infested with *Sa. polyphyllae*. Mite feeding activity damaged the integrity of the fungi-infected cadavers, which greatly disrupts fungal development and fungal sporulation. (C) Mite abundance on *Galleria mellonella* cadavers infected with *Metarhizium brunneum* or *Tr. afroharzianum*, freeze-killed cadavers, and pure fungal cultures over 18 days post-infection. Data represent mean numbers of mites ± SE ($n = 5$) replicates per treatment. Asterisks indicate significant differences between treatments at specific time points based on Tukey's honestly significant difference post hoc test (**$p < 0.01$, ***$p < 0.001$). Photo credit: M. Touray.

TABLE 1 Mycelial radial growth (in centimeters) of *Trichoderma afroharzianum*, antagonism against *Fusarium oxysporum*, and sporulation rate.

Treatments	Mycelial radial growth of *Tr. afroharzianum* (cm)				Antagonism	Sporulation
	3 days post-infection	5 days post-infection	7 days post-infection	10 days post-infection		
Tr. afroharzianum only	2.48 ± 0.61 ^{A}	5.46 ± 0.50 ^{A}	7.02 ± 0.07 ^{A}	7.02 ± 0.07 ^{A}	...	4^{A}
Tr. afroharzianum + *Fu. oxysporum*	2.54 ± 0.37 ^{A}	5.70 ± 0.58 ^{A}	7.06 ± 0.09 ^{A}	7.06 ± 0.09 ^{A}	1^{A}	4^{A}
Tr. afroharzianum + *Sa. polyphyllae*	2.69 ± 0.35 ^{A}	5.64 ± 0.57 ^{A}	6.93 ± 0.09 ^{A}	6.93 ± 0.09 ^{A}	...	3^{B}
Tr. afroharzianum + *Fu. oxysporum* + *Sa. polyphyllae*	2.94 ± 0.26 ^{A}	5.77 ± 0.37 ^{A}	6.73 ± 0.34 ^{A}	6.73 ± 0.34 ^{A}	1^{A}	3^{B}

Note: Data on mycelia growth are given as mean ± SE, data on antagonism of *Tr. afrohazianum* on *Fu. oxysporum* and sporulation of *Tr. afroharzianum* are presented as median. Different letters within a column indicate differences among medians ($p < 0.05$) using Dunn's multiple comparison test.

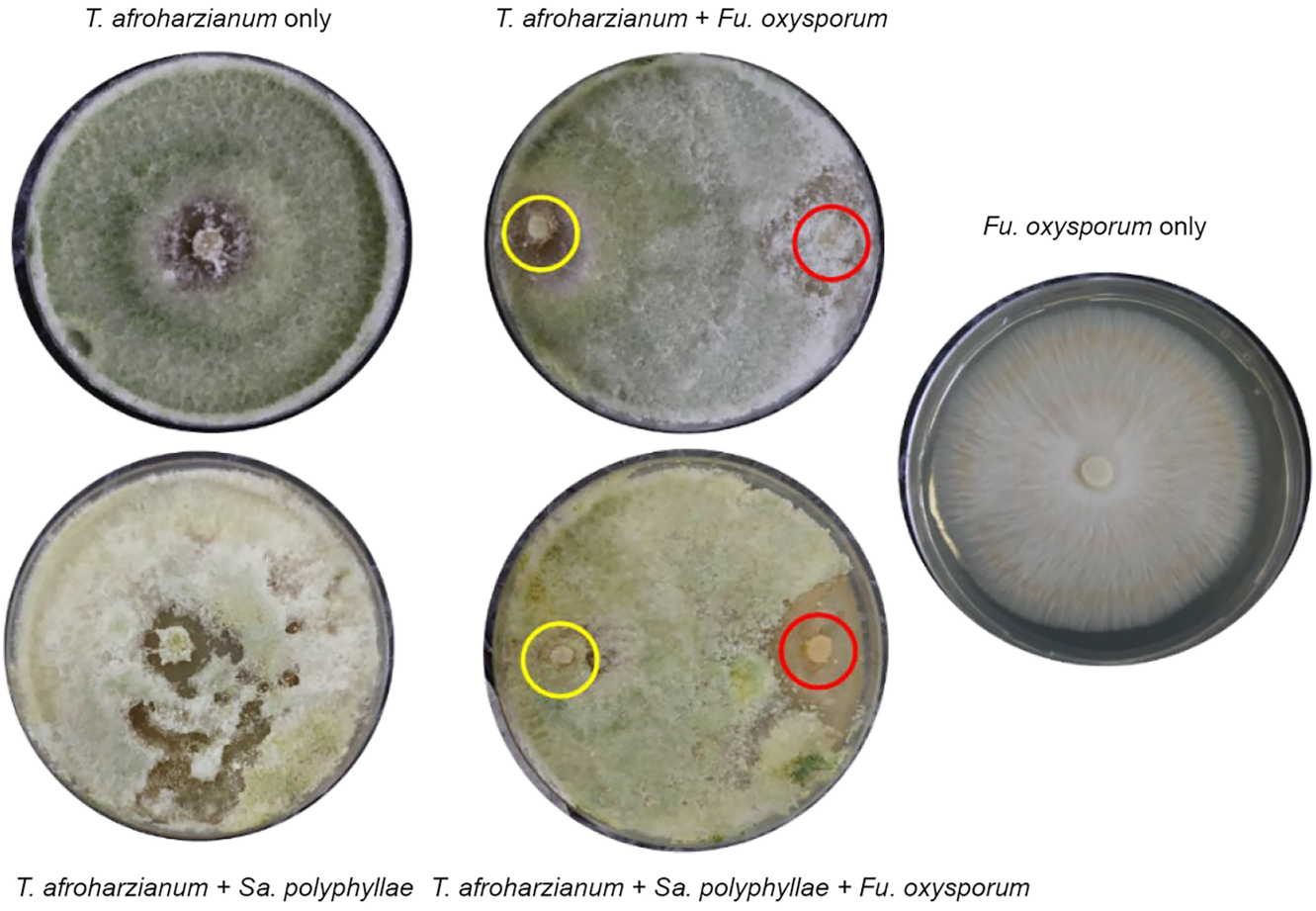

FIGURE 2 Antagonism of *Trichoderma afroharzianum* during confrontation assay with *Fusarium oxysporum*. The mites were observed grazing on the fungal mycelia, leading to the patchy growth (yellow and red circles indicate mycelial plugs of *Tr. afrohazianum* and *Fu. oxysporum*, respectively). Photo credit: M. Touray.

with fungi. Mite feeding activity was greater on *Trichoderma* cultures and *Trichoderma*-infected cadavers compared to *Metarhizium* cultures and *Metarhizium*-infected cadavers in Petri dish assays. The observation of mites carrying fungal spores suggests that mites can contribute to spore dispersal and thus fungal colonization, but this presents a potential cost to the mites themselves, possibly hindering movement, aggregation, or foraging efficiency. Also, mite feeding on infected cadavers caused visible damage to the cadaver integument and negatively impacted fungal sporulation. This damage can disrupt the fungal life cycle as insect resources are depleted before sporulation.

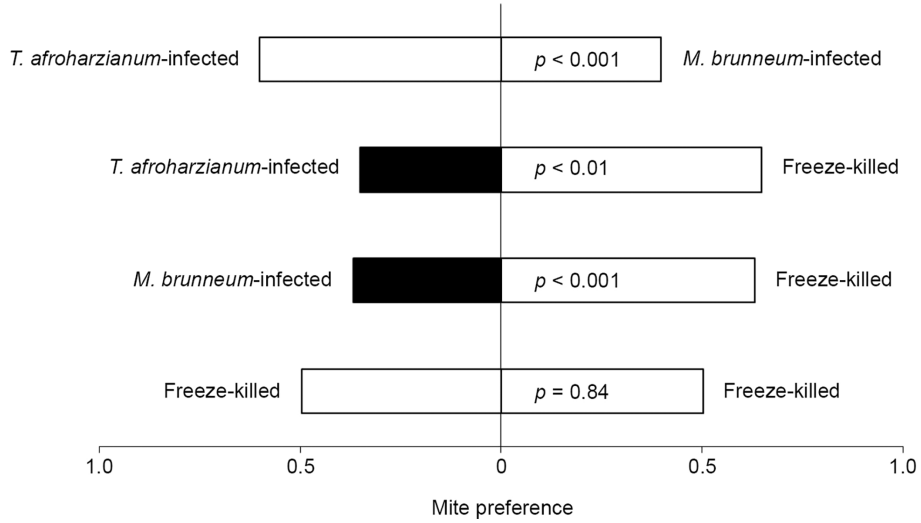

FIGURE 3 *Sancassania polyphyllae* preference between different freeze-killed and fungi-infected insect cadavers. Mite choice was assessed using a replicated G test of goodness of fit, based on the proportion of mites (adults and mobile developmental stages) observed on each of the two cadaver types.

Separately, the mycophagous mite *Tyrophagus putrescentiae* was found to survive and feed on pure cultures of seven EPF species: *Metarhizium flavoviride*, *Purpureocillium lilacinum*, *Marquandii*, *Cordyceps fumosorosea*, *Beauveria bassiana*, *Lecanicillium dimorphum*, and *Metacordyceps chlamydosporia*; but, feeding on *Metarhizium anisopliae* and *Metarhizium robertsii* proved lethal, causing mite mortality within 24 h and reaching 100% by 72 h (Ou et al., 2024).

Our preference assays revealed that mites generally preferred uninfected *G. mellonella* larvae, indicating that fungal infection negatively affects the palatability or nutritional quality of the prey once the fungi have started to grow. This avoidance behavior likely reduces mite consumption of infected cadavers, potentially limiting the dissemination of the fungal pathogen. However, the preference for *Trichoderma*-infected cadavers over *Metarhizium*-infected ones, despite the general avoidance of infected prey, suggests the involvement of additional factors. These could include differences in fungal or cadaver-derived volatile compounds, the presence of other microbial communities influencing attractiveness, or even nutritional differences between the two fungi. Further investigation into the chemical ecology of these interactions is needed. Moreover, the observed preference for *Fusarium* over *Trichoderma* in dual-culture assays is intriguing and suggests that the presence of *Fusarium* can influence mite behavior, potentially reducing their impact on *Trichoderma*. This has important implications for integrated pest management strategies. The ability of *Trichoderma* to suppress *Fusarium* and other soil fungi in soil due to its competitive saprophytic and mycoparasitic ability could indirectly affect mite populations by limiting their food resources, demonstrating the complex interactions between multiple fungal species. It also suggests that the presence of *Fusarium*, even if a pathogen itself, might alter the dynamics of the system in ways that affect *Trichoderma*'s biocontrol potential.

Mycophagous invertebrates (e.g., mites, springtails, nematodes, ants, and termites) are a key biotic factor influencing fungal community dynamics in the soil microbiome. Their grazing can exert selective pressure on fungi by stimulating the growth of less competitive fungi and by removing dominant fungal species (Crowther & A'Bear, 2012). Mites constitute a major component of soil mesofauna contributing substantially to both biomass and overall ecosystem function. Like most soil-dwelling Astigmata, *Sancassania* mites are fungivores/microbivores, feeding on fungi, nematodes, protozoans, rotifers, dead invertebrates, and decaying plant material, contributing to organic matter decomposition and nutrient cycling (Potapov et al., 2022). Furthermore, they can facilitate the dispersal of fungal spores, thereby influencing fungal reproduction and potentially triggering cascading effects on other organisms within the ecosystem (Bonkowski et al., 2009; Santamaria et al., 2023). This contrasts with some studies suggesting minimal impact of mesofauna grazing on overall fungal community composition (Crowther et al., 2011; Kaneko et al., 1998). While fungi possess substantial biomass and diverse biochemical defenses, making them generally resistant to grazing pressure (Wardle, 2006; Wardle & Yeates, 1993), our study demonstrates that mite grazing, particularly on

infected cadavers, can significantly impact fungal populations and, crucially, sporulation. This contrasts with some studies suggesting minimal impact of mesofauna grazing on overall fungal community composition (Crowther et al., 2011; Kaneko et al., 1998). However, our focus on specific interactions with biocontrol agents, where the impact of mite grazing on fungal reproductive success is paramount, is likely to explain this difference. Furthermore, the mobility of fungal spores, a critical factor in fungal ecology, is often mediated by invertebrates. A diverse array of invertebrates, including collembolans, beetles, lepidopterans, and various mite species, contribute to spore dispersal (Lin et al., 2019; Zimmermann, 2007). Phoretic mites, such as *Histiogaster anops* and *Macrocheles* sp., are known vectors of *M. brunneum* spores; however, both mites are also susceptible to *M. anisopliae* infection (Schabel, 1982). In contrast, *Folsomia candida* was not harmed by the tested EPFs (*Be. bassiana*, *M. anisopliae*, *Hirsutella* spp., and *Lecanicillium lecanii*) or the bacterium *Bacillus thuringiensis* (Broza et al., 2001). Potentially an adaptation to their shared soil habitat, resistance to EPF may allow soil invertebrates like collembolans and mites to exploit these fungi as a food source. This grazing pressure could also help regulate fungal proliferation in the soil (Broza et al., 2001; Christian et al., 1991; Rath, 1991).

While *Sancassania* mites have been recognized as beneficial in some contexts, such as nematode regulation (Sell, 1988), our findings highlight their potential to interfere with fungal biocontrol, similar to the reported interference by *Aphelenchoides* nematodes feeding on *Trichoderma harzianum* (Bae & Knudsen, 2001). *Sancassania polyphyllae* can also consume the infective juvenile stages of entomopathogenic nematodes and nematode-infected cadavers (Cakmak et al., 2010; Karagoz et al., 2007). Entomopathogenic fungi and nematodes are of significant socioeconomic importance within integrated pest management programs worldwide. These biocontrol agents are highly effective against certain arthropod pest species, and some strains have the potential to control white grubs and rhinoceros beetle (Koppenhöfer & Fuzy, 2003; Li et al., 2023; Malusá et al., 2020; Nasution et al., 2018; Ramanujam et al., 2021), with which astigmatid mites maintain phoretic relationships (Houck & OConnor, 1991). Although the use of fungi or nematodes in pest management is well established, they can interact with beneficial organisms, especially when they share hosts or interact within the food web. The application of these bioagents can impact mites, and conversely, mites can influence the efficacy of the bioagents (Cakmak et al., 2010; Karagoz et al., 2007). Our study adds to this body of evidence, demonstrating that mite feeding on fungi-infected cadavers can diminish the persistence and efficacy of fungal biocontrol agents. Our observations are likely only valid for low mite populations. Higher *Sa. polyphyllae* densities, different environmental conditions (e.g., temperature, humidity, soil type), or alternative hosts may yield different results.

In conclusion, this study reveals complex, context-dependent interactions between *Sancassania* mites and fungal biocontrol agents, highlighting the importance of considering these multitrophic interactions when developing and implementing biocontrol strategies. Future research should investigate the specific mechanisms driving these interactions, including the role of chemical cues, the influence of the broader soil microbiome, and the potential for synergistic or antagonistic effects with other soil organisms. A more holistic understanding of these complex relationships will be crucial for optimizing the use of fungal biocontrol agents in sustainable agriculture.

AUTHOR CONTRIBUTIONS

Mustapha Touray: Conceptualization; data curation; formal analysis; visualization; writing—review and editing. **Harun Cimen:** Visualization; formal analysis; writing—review and editing. **Ibrahim Cakmak:** Supervision; resources; formal analysis; validation; writing—review and editing. **Selcuk Hazir:** Supervision; resources; validation; formal analysis; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Touray, Cimen, et al., 2025) are available from Figshare: https://doi.org/10.6084/m9.figshare.28821242.

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