The ant, *Crematogaster* Lund, 1831 (Hymenoptera- Formicidae) engages in a mutualistic symbiosis with the mealybug, *Phenacoccus madeirensis* Green, 1923 (Hemiptera-Pseudococcidae) on ryegrass (*Lolium perenne*)

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Abstract

The mutually beneficial relationship between ants and mealybugs exemplifies a classic ecological mutualism, wherein mealybugs provide ants with honeydew, an energy-rich exudate, while ants offer mealy bug critical protection against natural enemies such as predators and parasitoid wasps, and facilitate their dispersal and colony maintenance. This protection enhances mealybug survival, reproductive success, and colony persistence, while simultaneously ensuring a continuous honeydew supply for ants. This symbiosis is regulated by complex biochemical and behavioural interactions, including signaling molecules in mealy bug secretions that trigger ant attendance and defence behaviours. Both ants and mealybug may selfishly manipulate one another, with mealybug modulating ant aggressiveness via dopamine in honeydew to maximize their own protection, and ants selectively tending mealybug morphs that yield higher-quality honeydew. Such reciprocal selfishness strengthens the mutualistic association and enhances fitness for both species. The ant- mealybug association is context-dependent, shaped by ecological variables such as colony size and environmental pressures, and can significantly affect mealybug population dynamics and development. Its ecological significance extends beyond the immediate organisms, influencing plant health, predator-prey interactions, and overall ecosystem stability.

Keywords: Mutualism, Ant-mealybug interactions, Biochemical signals, Dopamine, Honeydew

Introduction

Mutualistic interactions between ants and hemipteran insects, such as mealybugs, are well-documented ecological and evolutionary relationships that can significantly influence plant health and community dynamics. One well-known form of such interaction is trophobiosis, where ants establish symbiotic relationships with honeydew-producing hemipterans, including aphids, scale insects, and mealy bugs. The ant genus *Crematogaster* Lund, 1831 [12], is known for its tending behaviour towards sap-feeding insects, including mealy bugs, which produce honeydew, a critical carbohydrate resource for ants. In these associations, hemipterans serve as a valuable food source for ants, while ants, in return, protect them against predators and parasitoids, often facilitating higher population densities of the attended species (Way, 1963; Delabie, 2001) [24,5]. *Phenacoccus madeirensis* Green, 1923 [9], commonly known as the Madeira mealybug, is an invasive sap-feeding insect species frequently found on various host plants, including ryegrass (*Lolium perenne*) (Sullivan 1992, DiTomaso and Healy 2007) [22,6]. The genus *Crematogaster* is widely recognized for its strong mutualistic associations with honeydew-secreting insects across diverse habitats. These ants exhibit aggressive defensive behaviours and effectively deter natural enemies, thereby providing a survival advantage to their partners (Davidson *et al.,* 2003; Kudo *et al.,* 2021; Vela *et al.,* 2021) [4,11,23]. *Phenacoccus madeirensis*, a mealy bug of economic concern, infests a wide range of host plants, including grasses and ornamentals, and can cause significant damage through phloem feeding (Williams and Granara de Willink, 1992) [25]. Ryegrass (*Lolium perenne*), a commonly cultivated pasture and turf species, is a frequent host for mealy bug infestations. This mutualism is likely mediated through complex behavioural and biochemical mechanisms where ants protect mealy bugs from predators in exchange for honeydew (Shylesha and Joshi, 2012) [19].

Mealybugs control ant aggressive behaviour for their protection primarily through the secretion of honeydew, a sugary excretion that serves as a food resource for ants, fostering a mutualistic relationship. In this symbiosis, ants like *Crematogaster* species feed on the honeydew, thereby gaining nutritional benefits, and in return, they exhibit protective behaviours such as defending mealybugs from natural enemies including predators and parasitoids. The ant's aggressive tendencies are redirected towards protecting the mealybugs rather than preying on them, ensuring the mealybugs' survival and population growth (Marchiori *et al.,* 2023) [13]. Additionally, some ant species construct protective shelters or carton nests over mealybug colonies, physically shielding them from environmental stresses and predation. Ants patrol the host plants vigilantly and attack intruding predators, effectively reducing predation pressure on the mealybug populations. The intensity of ant defense behaviour can be influenced by the quality and quantity of honeydew offered, which sometimes contains biochemical compounds that modulate ant behaviour to enhance protection. Thus, mealybugs manipulate ant aggressive behaviour via nutritional rewards and possible chemical signaling to maintain a beneficial mutualistic relationship. This biochemical and behavioural control ensures the persistence and success of both the ants and the mealybugs in their shared environment, with significant implications for pest dynamics and ecosystem functioning in the habitats where they co-occur (Mgocheki and Addison, 2009; Marchiori *et al.,* 2023) [14,13]. The strong mealybug defense is linked to ant traits, including aggressiveness, worker abundance, responsive behaviour to threats, and the ability to exploit shelters, all influenced by food resource availability and environmental conditions. These traits collectively determine the efficacy of ant protection in mutualistic systems involving mealybugs. Several ant traits predict strong defense of mealybugs, including high aggression levels, large worker populations, and behavioural adaptations for tending. Their ability to construct or utilize shelters also enhances protection for mealybug colonies (Zhou *et al.,* 2012) [27]. Ant species with large, well-organized foraging workers respond more rapidly and vigorously to intruders, correlating with stronger defense. Furthermore, ants that increase their tending intensity in response to predator presence tend to provide more effective protection. Biochemical factors like the nutritional quality and quantity of honeydew from mealybugs influence the ants' motivation to defend, with better rewards driving higher aggression and attendance. Environmental factors such as temperature can also modulate these traits, with ants showing increased aggression and defense behaviour at warmer temperatures, further enhancing mutualism strength (Feng *et al.,* 2015; Zhou *et al.,* 2017) [7,26].

The ant species most aggressively defending mealybugs belong primarily to the Formicidae family, with notable examples including ghost ants (*Tapinoma melanocephalum*) and fire ants (*Solenopsis spp*.). Ghost ants exhibit highly aggressive behaviour toward natural predators of mealybugs, such as lady beetle larvae and parasitoids, providing strong protection that significantly increases mealybug survival rates. This aggressive defense includes physical attacks and chemical secretions that deter or repel predators and parasitoids, thereby reducing biological control effectiveness (Zhou *et al.,* 2014; Feng *et al.,* 2015) [28,7]. Research has also shown that more aggressive ant species tend to provide better protection for mealybugs and other hemipterans, correlating ant aggressiveness with enhanced mutualistic benefits for the mealybugs. This increased aggression is typically fuelled by the nutritional rewards ants receive from honeydew, which incentivizes vigilant and forceful defensive behaviours. Accordingly, ant species that can mobilize more workers and exhibit higher aggression levels create more effective defense systems around mealybug colonies. Thus, ghost ants, fire ants, and other aggressive Formicidae species are recognized as the most effective defenders of mealybugs, utilizing a combination of aggressive physical behaviour and chemical signals to protect their honeydew-producing partners from predation and parasitism (Buckley and Gullan, 1991; Mgocheki and Addison, 2009) [1,14].

Ant's reliance on honeydew as a primary carbohydrate source significantly influences their tending behaviour toward honeydew-producing insects like mealybugs. Honeydew acts as a predictable and renewable food resource that attracts ants to hemipteran insects, motivating ants to protect and tend these insects to ensure a continuous supply of this valuable nutrient. The presence of honeydew leads to increased ant aggression towards predators and parasitoids, enhancing the protection provided to the mealybugs and thereby reinforcing the mutualistic relationship (Styrsky and Eubanks, 2007) [21]. Moreover, the quality and quantity of honeydew impact the intensity of ant tending. For instance, increased amino acid concentrations in honeydew can heighten ant attraction and care levels, although this may come at a cost to the producing insect's growth and fecundity. Behavioural responses, including recruitment and foraging activity on host plants, are also triggered by the detection of honeydew, such as when ants sense scattered droplets or flicked honeydew, prompting them to climb onto plants and engage in tending. These interactions drive broader ecological effects as ant attendance can modify local arthropod community dynamics by suppressing other herbivores while simultaneously potentially exacerbating plant damage caused by protected hemipterans (Claro and Oliveira, 1996; Styrsky and Eubanks, 2007) [3,21].

Materials and Methods

The study area and samples were collected from Isabella Thoburn College, Lucknow (Lat. 26.8721450 and Long. 80.9445130). The experiment will focus on the mutualistic interaction between *Crematogaster* Lund, 1831[12], ants and the mealy bug *Phenacoccus madeirensis* Green, 1923, on ryegrass (*Lolium perenne*). Experimental Design, including counting of the number of ants per mealy bug on each alternate day (August to September, 2025), defensive behaviour frequency against natural enemies, mealybug survival and colony growth rate, and plant health parameters. Ant's aggressive responses will be quantified by natural predator insects and the ant's defensive actions. The mealybugs were identified and preserved in glass tube containing 70% ethanol for further observation and photography (Sirisena *et al.* 2013; Joshi *et al.,* 2021) [20,10].

Results and Discussion

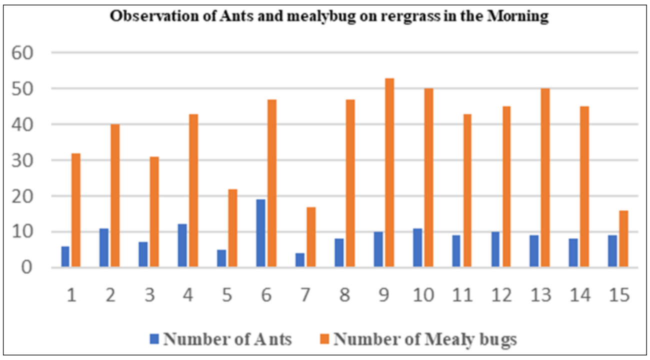
Mutualistic interactions between ants and hemipteran insects such as mealybugs constitute ecologically significant relationships impacting plant health and community dynamics. In this study, the ant genus *Crematogaster spp.* Lund, 1831, demonstrated strong tending behaviour towards the mealybug *Phenacoccus madeirensis* Green, 1923[9], on ryegrass (*Lolium perenne*), supporting the well-established concept of trophobiosis where ants obtain carbohydrate-rich honeydew in exchange for protection. The observed aggressive defense by *Crematogaster* ants aligns with previous findings describing their effective deterrence of natural enemies, facilitating increased survival and population growth of attended mealybugs. Such interactions are reinforced by biochemical signals and behavioural mechanisms mediating ant aggression and tending intensity (Delabie, 2001; Davidson *et al.,* 2003; Shylesha & Joshi, 2012; Vela *et al.,* 2021) [5, 4, 19, 23].

The body of the adult female *Phenacoccus madeirensis* Green, 1923[9] is oval and somewhat flattened dorsoventrally, exhibiting a grayish-green coloration. Fully grown females have reddish legs and antennae, and the entire body is covered with a thin layer of white, mealy wax. Distinctive features include two longitudinal white lines along the submarginal area and two depressed regions around the dorsal midline, causing the middorsal line to appear slightly elevated. There are 4–5 short wax outgrowths arranged horizontally across each abdominal and thoracic segment, as well as 18 pairs of lateral wax filaments with the posterior pairs being the longest and reaching about one-eighth or less of the body length (Figure 1B). The ovisac is created from thick white wax that extends in an elongated form from the abdomen, containing yellow eggs (Papadopoulou and Chryssohoides**,** 2012; Shylesha and Joshi, 2012; Joshi *et al.,* 2021) [15,19, 10].

Observations show a positive association between the number of *Crematogaster* ants and *Phenacoccus madeirensis* mealybugs per sampling event in ryegrass fields. Higher mealybug counts consistently coincide with higher ant counts across the observed samples. For instance, observational count with more than 40 mealybugs tend also to host 10–12 ants per sampling (Figure 1), whereas observational count with fewer mealybugs (16–22) have 4–6 ants (Figure 1). The mealybug numbers range from as low as 16 to as high as 53, while ant numbers range from 4 to 12 (Table 1 and Graph 1). It suggests that higher mealybug populations tend to coincide with higher numbers of ants, indicating a positive association reflective of mutualistic behaviour. The highest mealybug count (53) corresponds to one of the highest ant counts (10), supporting the idea that ants tend to aggregate around larger mealybug colonies for their honeydew resource. This trend points to ants actively tracking mealybug density and preferentially tending high-density colonies, likely due to increased honeydew availability. Conversely, lower mealybug populations often have fewer ants present (Table 1). However, there is some variability suggesting other ecological factors may influence these populations, such as predation pressure, availability of alternative food sources, or microhabitat conditions that affect ant attendance. The data also reveals instances where moderate mealybug counts correspond with low ant presence, indicating that mealybug protection by ants is not solely dependent on mealybug abundance but could involve additional behavioural or chemical cues. Such a pattern is typical for ant-ant-hemipteran mutualism systems, where the strength of ant attendance is modulated by carbohydrate rewards from mealybugs. The consistent presence of ants in higher numbers with increasing mealybug populations demonstrates that ants allocate foraging and defensive effort to areas providing maximal nutritional benefit. The morning observations align with established knowledge that *Crematogaster* ants tend and protect mealybugs in a density-dependent manner, concentrating more workers in areas with abundant honeydew. This enhanced tending behaviour provides greater protection for mealybugs from predators and parasitoids, further reinforcing the positive mutualistic relationship and sustaining high mealybug populations between the two species on ryegrass plants.

Table 1: Observational number of ants and mealybugs on ryegrass

Observation in the Morning		
S. No.	**Number of Ants**	**Number of Mealy bugs**
1	6	32
2	11	40
3	7	31
4	12	43
5	5	22
6	19	47
7	4	17
8	8	47
9	10	53
10	11	50
11	9	43
12	10	45
13	9	50
14	8	45
15	9	16



Graph 1: Showing variation in numbers of ants and mealybugs on ryegrass

The defensive behaviours displayed by ants to protect mealybugs were frequently patrolling the area around mealybug colonies and directly attacking approaching predators and parasiticides, such as lady beetle larvae and tiny wasps, by biting, stinging, or using alarm pheromones to recruit more ant defenders (Mgocheki and Addison, 2009; Parrilli *et al.,* 2021) [14,16]. Ants may spray formic acid or other chemicals to deter predators, especially when faced with persistent attackers. Aggressive ant activity often causes biological control failures, as they interfere with or physically remove parasitoids and predators from infested plants, lowering the effectiveness of natural enemy introductions (Parrilli *et al.*, 2021) [16]. In some cases, ants physically move mealybugs to safer locations if a threat is detected, ensuring the continuity of honeydew production (Chalise, 2023) [2]. Ants maintain high vigilance and remain on guard around honeydew resources (Figure 1 B), especially the most productive mealybug colonies, for rapid response to threats (Zhou *et al.,* 2012; Marchiori *et al.,* 2023) [27,13].

Mealybugs manipulate ant behaviour through nutritional rewards, primarily honeydew secretion, that encourage ants to redirect their aggressiveness towards defending them instead of preying on them (Marchiori *et al.*, 2023) [13]. Ant traits such as aggressiveness, worker abundance, and threat responsiveness directly correlate to the efficacy of mealybug defense, with environmental variables like temperature further enhancing mutualism strength (Feng *et al.,* 2015; Zhou *et al.,* 2017) [7, 26]. The most aggressive defenders belong largely to the Formicidae family, including ghost ants (*Tapinoma melanocephalum*) and fire ants (*Solenopsis spp.),* noted for their robust physical and chemical defense strategies (Zhou *et al.,* 2014; Feng *et al.,* 2015) [28, 7].

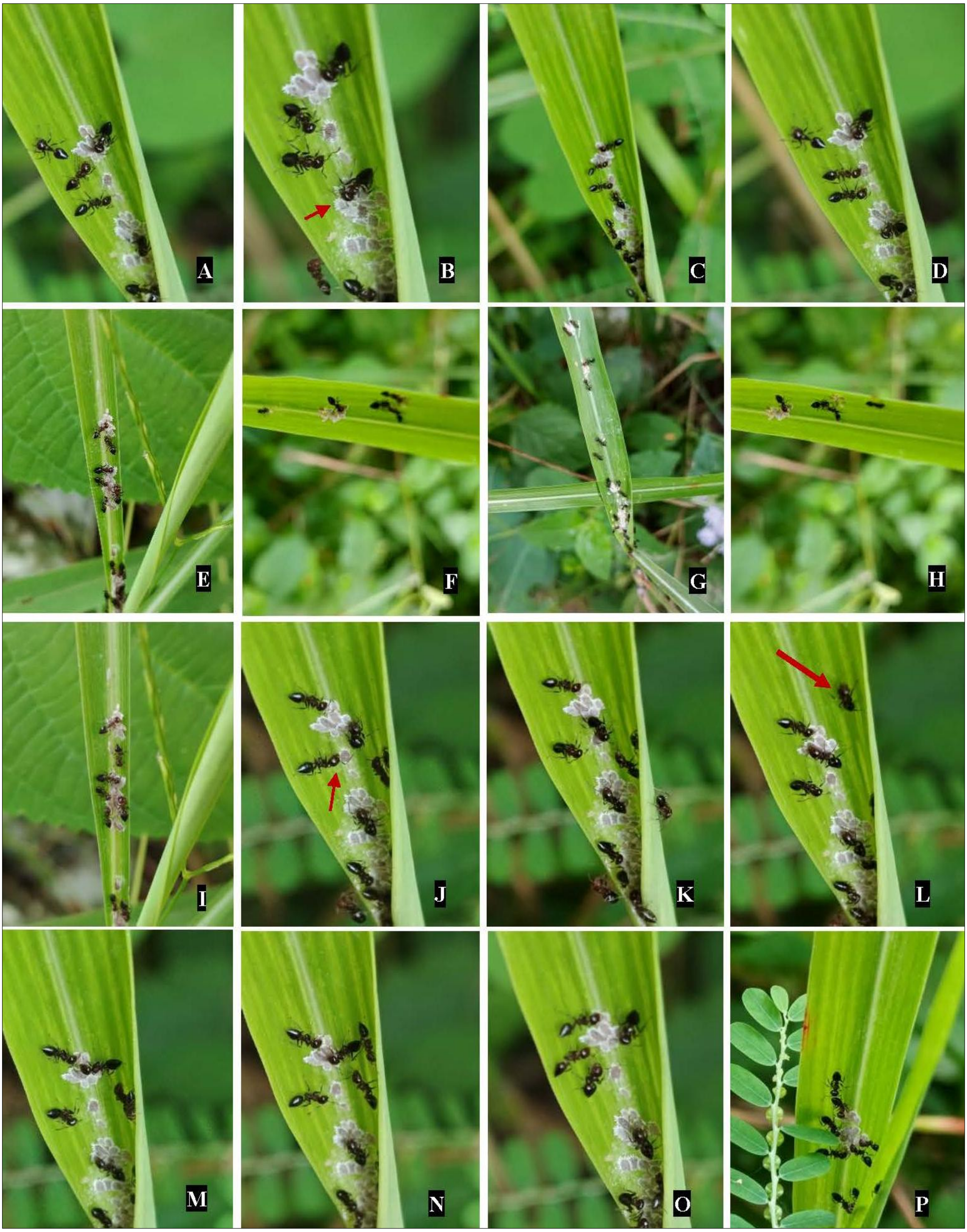


Fig 1: A-P Variable number of Ants and Mealybugs observed on ryegrass. B, J -Ant receiving honeydew from mealybugs. L-vigilant and patrolling behaviour of ant

The honeydew reward influences ant guarding intensity by providing essential nutrients and chemical signals that increase ant attraction and aggressiveness, leading to stronger protection of honeydew-producing insects like mealybugs. Honeydew reward strongly influences ant guarding intensity primarily through chemical and nutritional cues. The sugar and amino acid composition of honeydew, especially the presence of specific sugars like sucrose and compounds such as dopamine, serve as stimulants that increase ant foraging preference, attendance, and aggression toward predators of honeydew-producing insects like mealybugs. Research shows that dopamine present in aphid and mealybug honeydew can increase the aggressiveness of attending ants in a dose-dependent manner by modulating neural pathways related to defensive behaviour. Without these biochemical signals, ants show lower aggression and less guarding activity. The quantity and quality of honeydew thus regulate how intensely ants protect their mutualistic partners; higher sugar concentration and favourable chemical cues promote increased tending and more vigorous defense. Moreover, ants prioritize their foraging and protection efforts on honeydew sources with higher sucrose levels, as sucrose provides greater energetic benefits. Studies on ghost ants and fire ants demonstrate that sugar composition shapes ant visitation frequency and defensive responses, thereby modulating the strength of ant-mediated protection of mealybugs (Zhou *et al.,* 2015; Kudo *et al.,* 2021) [29,11].

Honeydew is a sugar-rich secretion produced by mealybugs, as they ingest large volumes of phloem sap to obtain essential nutrients. Its primary chemical constituents include various sugars mainly glucose, fructose, and sucrose and small amounts of amino acids, organic compounds, and inorganic salts. The specific composition can vary depending on the insect species, host plant, and environmental factors. For ants, honeydew acts as a vital carbohydrate resource fulfilling their energy needs. Sugars in honeydew provide readily metabolizable energy essential for ant activities such as foraging, colony maintenance, and defensive behaviours. Amino acids present in honeydew, although in smaller quantities, contribute to ants' protein requirements for growth and reproduction, supplementing their more carnivorous diet (Fischer and Shingleton 2001; Pringle *et al.,* 2014) [8, 17]. The continuous availability of honeydew stabilizes mutualistic relationships by incentivizing ants to protect hemipteran insects from natural enemies. Nutritional preferences seem to favour sucrose-rich honeydews, which maximize energy intake, and a mixture of sugars and amino acids aligns with ants' biochemical requirements. Variation in honeydew chemistry, influenced by host plant genetics and insect metabolism, can thus affect ant colony health, behaviour, and ecological performance through these nutritional pathways (Claro and Oliveira, 1996; Pringle *et al.,* 2014; Styrsky and Eubanks, 2007) [3, 17, 21].

Conclusion

This study demonstrates that the mutualistic interaction between *Crematogaster* ants and *Phenacoccus madeirensis* mealybugs on ryegrass is a dynamic and ecologically impactful relationship characterized by reciprocal benefits that reinforce the fitness of both partners. The findings reveal a clear positive association between mealybug density and ant abundance, with *Crematogaster* ants displaying heightened defensive and tending behaviours in response to increases in honeydew-producing mealybug populations. This density-dependent allocation, driven primarily by the nutritional and biochemical composition of honeydew, ensures both the persistence of large mealybug colonies and a sustained carbohydrate supply for ant colonies. Ants exhibit a range of specialized defensive behaviours, including patrolling, direct attacks, alarm signaling, chemical defense, and strategic relocation to protect their honeydew producers from natural enemies, thereby enhancing mealybug survival and population growth. The mutualism's strength and ecological significance are further supported by the ability of ants to modulate their protection according to honeydew quality and quantity, alongside environmental factors such as microclimate and alternative food sources. This behavioural plasticity, underpinned by evolved nutritional preferences and efficient signaling pathways, highlights the adaptive value of mutualistic associations in shaping the structure and resilience of insect communities within grassland agroecosystems.

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