

Plant species specificity of ant–plant mutualistic interactions: Differential predation of termites by *Camponotus crassus* on five species of extrafloral nectaries plants

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Funding information

Fundação de Amparo à Pesquisa do Estado de Minas Gerais; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: C001; Conselho Nacional de Desenvolvimento Científico e Tecnológico

Associate Editor: Jennifer Powers

Handling Editor: Anand Osuri

Abstract

There is increasing evidence that the outcomes of mutualistic interactions between ants and plants bearing extrafloral nectaries (EFNs) are context-dependent. In particular, the total number, density, and size of EFNs, as well as the abundance and identity of ants attending host plants, are considered as key factors determining the nature and strength of ant–EFN-bearing plant interaction. Although many previous studies have investigated context-dependency in ant–plant protection mutualisms mediated by EFNs, few have tested whether the protective behavior of ants varies among sympatric plant species. In this study, we performed a field experiment to investigate the predatory behavior of a dominant ant species (*Camponotus crassus*, Formicinae) among five EFN-bearing plant species growing in the Brazilian savanna. In particular, we studied the variation in the ant abundance, termite predation, and time spent to find termites of *C. crassus* among the plant species, and further analyzed whether this variation could be related to the extrafloral nectar volume and sugar concentration of each plant species. We found that abundance and termite predation of *C. crassus* markedly varied among plant species. Specifically, *C. crassus* ants were significantly more abundant, active, and protective in *Qualea multiflora*, the plant species that produced significantly higher volumes and sugar concentrations of nectar. Overall, our results suggest that variation in extrafloral nectar volume and sugar concentration can result in plant species specificity of defensive behavior of a dominant foliage-dwelling ant in the Brazilian savanna.

Abstract in Portuguese is available with online material.

KEYWORDS

ant, biotic defense, Brazil, *Camponotus crassus*, Cerrado, extrafloral nectar, indirect defense, plant mutualism, protective effectiveness

1 | INTRODUCTION

Over the last century, the study of trophic interactions within communities has represented a central goal to understand ecosystem dynamics and processes (Dyer, 2011; Lindeman, 1942; May, 1973; Price et al., 1980). Antagonistic (including predation, parasitism, and disease) and mutualistic interactions are two of the most common trophic interactions in nature (Bronstein, 2015; Del-Claro & Torezan-Silingardi, 2021; Minelli, 2008). Antagonism is the ecological interaction between two organisms in which one benefits at the expense of the other. By contrast, mutualism is the ecological interaction between two or more species where each species has a net benefit (Boucher et al., 1982; Bronstein, 1994, 2015). Generally, one partner in the mutualism provides a sort of “service” (e.g., pollen transfer and protection), and the other one provides in return a sort of “reward” (e.g., food and housing; Bronstein, 1994).

Ants are one of the most successful and ecologically important groups of terrestrial insects (Hölldobler & Wilson, 1990; Lach et al., 2010). By acting as predators or mutualists, ants play a key role in shaping ecosystem structure and function (e.g., Heil & McKey, 2003; Styrsky & Eubanks, 2007). Ants commonly establish mutualistic interactions with myrmecophilous plants (Calixto et al., 2018; Ridley, 1910). In these interactions, plants produce food rewards (e.g., extrafloral nectar) that attracts ants, which in turn protect plants against herbivores (Calixto et al., 2015, 2018; Del-Claro et al., 2016, 2018). The most common reward offered by plants is the extrafloral nectar, a carbohydrate-rich liquid produced by specialized glands or tissues called extrafloral nectaries (EFNs) (Pires et al., 2017; Weber et al., 2015). This nectar is fundamental for ant larval growth, ovary development and egg production in ant queens, and metabolism and sperm production in ant adults (Byk & Del-Claro, 2011; Calixto et al., 2021; Nation, 2015). In addition to ant performance traits, numerous studies have demonstrated that the abundance and nutritional composition of EFNs also influence several traits associated with ant defensive behavior such as ant abundance (Bixenmann et al., 2011; Blüthgen & Fiedler, 2004; Calixto et al., 2021), aggressiveness (Fagundes et al., 2017), foraging patterns (Blüthgen & Fiedler, 2004; Lange et al., 2017), and prey choice (Wilder & Eubanks, 2010). By influencing ant defensive behavior, the abundance and chemical composition of EFNs might determine the outcomes of ant–plant mutualistic interactions (Baker-Méio & Marquis, 2012; Calixto, Lange, Bronstein, et al., 2021; Del-Claro et al., 2018; Fagundes et al., 2017).

Mutualistic interactions between ants and EFN-bearing plants often depend on both the biotic (e.g., ant species and plant species) and abiotic (e.g., rainfall, temperature, and humidity) context. For instance, the abundance and identity of ants attending the host plant (Fagundes et al., 2017; Rudgers & Strauss, 2004), as well as the total number, density (number per specific plant structure, e.g., leaves), and size of EFNs and herbivore pressure (Baker-Méio & Marquis, 2012; Calixto, Lange, Bronstein, et al., 2021; Calixto, Novaes, et al., 2021; Fagundes et al., 2017; Fuente & Marquis, 1999; Rudgers & Strauss, 2004), are known to determine the nature and strength of

ant–plant mutualisms. Although many previous studies have investigated context-dependency in ant–plant protection mutualisms mediated by EFNs, few have tested whether the protective behavior of ants varies among sympatric plant species (Apple & Feener, 2001; Baker-Méio & Marquis, 2012; Fagundes et al., 2017). EFN-bearing plant species often differ in physical characteristics (structure, shape, and size) and productivity (volume and nutritional composition) of EFNs (Koptur, 1994; Lange et al., 2017), resulting in turn in differences in ant protective behavior among plant species (Baker-Méio & Marquis, 2012; Fagundes et al., 2017). In a correlational study, Fagundes et al. (2017) found that the degree of ant protection was positively associated with sugar concentration of nectar and such protective effectiveness varied markedly among 10 plant species growing in an area of Rupestrian Grasslands (Brazil). In another correlational study, Baker-Méio and Marquis (2012) found that EFNs were larger, produced more nectar and attracted more ants in one variety of the *Chamaecrista desvauxii* complex (Leguminosae) than in other two co-occurring varieties in a Brazilian savanna.

In this study, we performed a field experiment to investigate the protective behavior (i.e., abundance and predation) of a dominant ant species (*Camponotus crassus*, and Formicinae) among five EFN-bearing sympatric plant species of the Brazilian savanna (called Cerrado). We hypothesized that *C. crassus* protective behavior is determined by the volume and sugar concentration of the EF nectar. Because the studied plant species exhibit large differences in EFN production and structure (see Table 1), we predict that *C. crassus* would be more protective in plants that offer a higher level of volume and sugar concentration. Previous studies investigating variation in ant protective behavior among sympatric EFN-bearing plant species have considered the additive effects of different ant species on herbivory and plant fitness (Apple & Feener, 2001; Baker-Méio & Marquis, 2012; Fagundes et al., 2017; Lange & Del-Claro, 2014). By comparing the protective behavior of only one ant species in several sympatric plant species, we minimize differences in plant defense due to variation in the ant community attending host plants. Overall, this study builds toward a better understanding about the specificity of ant–plant mutualistic interactions mediated by EFNs.

2 | MATERIAL AND METHODS

2.1 | Study area, plant species, and ant species

The fieldwork was conducted in the Ecological Reserve of the Clube de Caça e Pesca Itororó de Uberlândia (18°58'59"S; 48°17'53"W) in Uberlândia, Brazil. The reserve is located in a tropical savanna ecoregion (called Cerrado) (Oliveira & Marquis, 2002) and has about 200 ha of cerrado sensu stricto vegetation (specific vegetation of Cerrado). The cerrado sensu stricto vegetation contains palm swamp areas, open areas with shrubs and small trees, and more enclosed areas with trees reaching up to 15 m in height (Del-Claro et al., 2019). In this region, there is a marked rainy season from October to March and a marked dry season from April to September (Alvares

TABLE 1 Extrafloral nectary production (volume and sugar concentration) and structure (size and type) of five extrafloral nectary-bearing plant species growing in the Brazilian cerrado. Data were collected in a previous study (Lange et al., 2017). Volume and sugar concentration are represented as the production per day. Different letters indicate significant differences among plant species by Estimated Marginal Means.

Species	Volume (μL)	Sugar (% Brix)	Length*Width (mm^2)	Type
<i>Banisteriopsis malifolia</i>	0.24 \pm 0.14 ^a	1.59 \pm 1.24 ^a	2.01 \pm 0.79 ^b	Elevated
<i>Lafoensia pacari</i>	0.85 \pm 0.40 ^{abc}	5.25 \pm 2.75 ^{abc}	3.62 \pm 1.25 ^c	Elevated
<i>Ouratea spectabilis</i>	1.27 \pm 1.71 ^{bc}	4.83 \pm 2.65 ^{ab}	0.93 \pm 0.62 ^a	Flattened
<i>Qualea multiflora</i>	2.13 \pm 2.06 ^c	12.0 \pm 10.8 ^c	2.63 \pm 0.70 ^{bc}	Elevated
<i>Stryphnodendron polyphyllum</i>	0.93 \pm 0.91 ^{ab}	7.06 \pm 5.66 ^b	7.30 \pm 2.80 ^d	Elevated

et al., 2013; Calixto, Novaes, et al., 2021; Novaes et al., 2020). The mean annual temperature varies from 18 to 28°C, and annual rainfall varies from 800 to 2,000 mm (Ferreira & Torezan-Silingardi, 2013).

For this study, we selected five of the most abundant EFN-bearing woody species in our study area (Appolinario & Schiavini, 2002): *Banisteriopsis malifolia* Nees & Mart. (Malpighiaceae), *Lafoensia pacari* (A. St.-Hil.) (Lythraceae), *Ouratea spectabilis* (Mart.) Engl. (Ochnaceae), *Qualea multiflora* (Mart.) (Vochysiaceae), and *Stryphnodendron polyphyllum* (Mart.) (Fabaceae). All the plant species exhibit active EFNs on newly flushed leaves at the beginning of the rainy season (September–October) (Calixto, Novaes, et al., 2021; Lange et al., 2013) and largely vary in production (volume and sugar concentration) and structure (size and type) of EFNs (Table 1). Because plants continuously produce new leaves, EFNs are present on the same individual plants for months. Rainfall events rarely remove extrafloral nectar.

The EFNs of these plant species are frequently visited by *Camponotus crassus* (Formicinae) ants (Anjos et al., 2017; Lange et al., 2017, 2019; Nahas et al., 2012; Pires et al., 2017). This ant species exhibits an aggressive behavior against insect herbivores (Fagundes et al., 2017; Lange et al., 2019; Sousa-Lopes et al., 2020), which usually results in lower levels of herbivory and higher fruit production compared with plants without ants (Calixto et al. in review). Due to its numerical abundance and aggressive behavior, *C. crassus* is the dominant ant species on EFN-bearing plants in the Cerrado (Anjos et al., 2017; Lange et al., 2017, 2019; Nahas et al., 2012; Pires et al., 2017). Only few other ant species (usually subordinate and docile ants) are allowed to forage on the same plant individuals where *C. crassus* monopolizes (Calixto et al. in review; Fagundes et al., 2016). Therefore, fitness (e.g., herbivory rate and fruit production) of EFN-bearing plants hosting *C. crassus* ants would largely depend on the protective behavior of this ant species.

2.2 | Data collection

In October 2017, that is, during the rainy season and when most plants had active EFNs (Calixto, Novaes, et al., 2021; Lange et al., 2013), we selected 20 individuals of each plant species ($n = 100$ individuals) with similar height (1.5–2 m), separated by at least 10 m, and dominated by *C. crassus* ants. In each individual plant, we selected the first leaf of an

apical branch without marks of herbivore damage. Between 09:00 h and 11:00 h, we added an alive worker of *Nasutitermes* sp. (Isoptera: Termitidae) collected from three nests to conduct a termite predation experiment. Termites were gently captured with the help of tweezers, and without hurting them, they were placed on the plants. The predation of termite baits has been widely used as a proxy of ant effectiveness against herbivores in many plant taxa (Anjos et al., 2017; Apple & Feener, 2001; Cruz et al., 2018; Fagundes et al., 2017; Oliveira, 1997; Oliveira et al., 1987; Pacelhe et al., 2019; Raupp et al., 2020; Saks & Carroll, 1980). In order to avoid biases on encounter time, we only added termites on plants with at least one individual of *C. crassus* foraging on it, and when all *C. crassus* individuals patrolling the plant were at least 30 cm away from the selected leaf.

After adding the termite, we waited for 30 sec until acclimatization and started the observation. We observed termites for a maximum of 15 min (if there was no predation event during that time window), and during this time, we counted total *C. crassus* ant abundance on the whole plant, the time spent by *C. crassus* ants to find the termite, and the termite survival probability (1 = alive and 0 = preyed) or the termite predation (1 = preyed and 0 = not preyed) by *C. crassus* ants. We assume that there were no major changes in the total number of ants during the 15 min of experiment. Moreover, *C. crassus* ants usually do not remove termites from the plant (take and throw the termite out of the plant), but they prey on them (Lange et al., 2019). Therefore, the termite predation parameter was represented by the act of attacking and taking termites to the nest by ants. Because we aimed at evaluating the time spent by ants to find termites and (after finding them) the predation/removal rate, termites have to remain on the plants to be found by ants. If the termite fell from the plant, we discarded the observation and started again.

2.3 | Data analysis

In order to investigate ant abundance variation among plant species, we performed a generalized linear model (GLM) where we included the total abundance of *C. crassus* as a response variable and plant species as the explanatory variable. To control for overdispersion in this model, we used a negative binomial distribution. In order to investigate whether increasing *C. crassus* abundance on plants also

increases the probability of termite predation, we performed a GLM where we included termite predation rate as a response variable (binomial error) and the abundance of *C. crassus* as the explanatory variable. Models were fitted using the package “stats” followed by a likelihood-ratio test using the package “car” (Fox & Weisberg, 2018) in R software 4.0.0 (R Core Team, 2020). We then conducted posteriori tests with estimated marginal means using the package “emmeans” (Lenth, 2020).

Termites were observed for a maximum of 15 min (when there is no predation event), but we divided our analysis in 5, 10, and 15 min (when possible, since termites can be preyed any time during the 15 min) after adding the termite to quantify whether ant protective behavior also varied temporally among plant species. This analysis over time is important to show whether ants maintain the same pattern of effectiveness over time among species. In order to investigate variation in ant predatory activity (a variable associated with ant aggressiveness) among plant species, we performed a GLM where we included termite survival probability (1 = alive and 0 = preyed) over time (at 5, 10, or 15 min) as response variable and plant species as the explanatory variable. For this analysis, we used the Weibull distribution and the G-rho family of Harrington and Fleming (1982) in the package “survival” (Therneau, 2015) in R. Then, we conducted pairwise comparisons with Log-Rank test and p-value correction of Benjamini and Hochberg (1995) using the package “survminer” (Kassambara & Kosinski, 2018).

Finally, we combined three parameters evaluated in our study into an index to estimate the protective effectiveness based on the landscape analysis of effectiveness (Rodríguez-Rodríguez et al., 2013; Schupp et al., 2010) every five minutes of evaluation (at 5, 10, and 15 min). We calculated the protective effectiveness of *C. crassus* ants for each plant species by multiplying the quantitative components (QNC) by the qualitative components (QLC) (Rodríguez-Rodríguez et al., 2013; Schupp et al., 2010). The QNC was based on the total abundance of *C. crassus* ants on each individual plant, and the QLC was based on the multiplication of the inverse of the time spent by ants (in minutes) to find the termite by the percentage of termites preyed upon by an ant (0 or 100%). Then, we plotted the protective effectiveness of *C. crassus* ants for each plant species in a biplot with isoclines. In order to investigate variation in ant protective effectiveness (a variable associated with ant aggressiveness) among plant species, we conducted a GLM analysis where we included protective effectiveness as a response variable and plant species as the explanatory variable.

3 | RESULTS

Total ant abundance differed among plant species (GLM: $\chi^2 = 36.025$, $p < 0.001$, McFadden pseudo $R^2 = 0.09$; Figure 1a). Mean ant abundance per plant was greater for *Q. multiflora* (4.40 ± 2.7 ; mean \pm SD) than for *S. polyphyllum* (2.35 ± 1.92), *B. malifolia* (1.70 ± 1.0), and *L. pacari* (1.6 ± 0.7), but not than *O. spectabilis* (3.05 ± 1.67) (Figure 1a). Mean ant abundance per plant did not

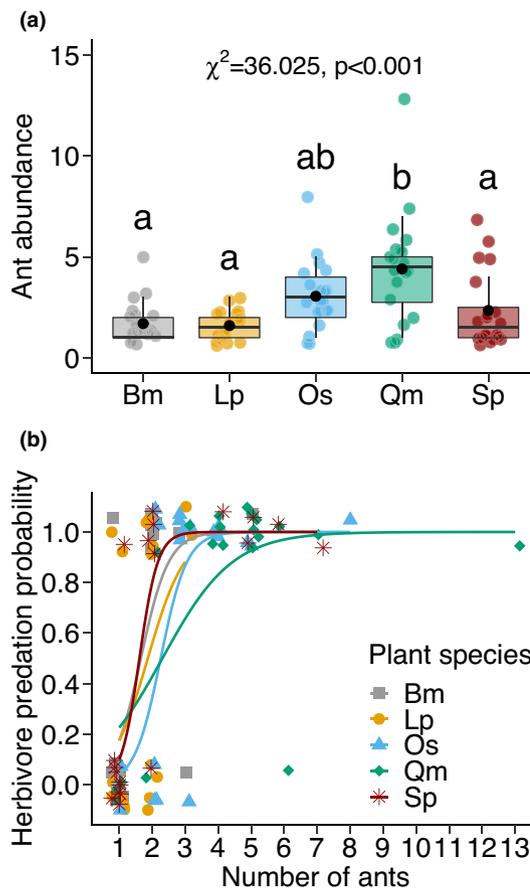


FIGURE 1 Variation in (a) abundance of *Camponotus crassus* ants and (b) herbivore (termite) predation probability according to the number of ants among five extrafloral nectary-bearing plant species growing in the Brazilian cerrado. In the first panel (a), different letters indicate significant differences ($p < 0.05$) among plant species, and black dots represent the mean. In the panel (b), we used a vertical jitter function to decrease overlapping of points and make the figure clearer, although points can assume only 0 or 1 value. Bm—*Banisteriopsis malifolia*, Lp—*Lafoensia pacari*, Os—*Oureatea spectabilis*, Qm—*Qualea multiflora*, and Sp—*Stryphnodendron polyphyllum*

differ between *O. spectabilis*, *S. polyphyllum*, *B. malifolia*, and *L. pacari* (Figure 1a). We observed a significant increase in termite predation probability as ant abundance increased for all plant species (*B. malifolia*: $\chi^2 = 5.00$, $p < 0.05$, estimated coefficient $\beta_1 = 2.370$; *L. pacari*: $\chi^2 = 3.89$, $p < 0.05$, $\beta_1 = 1.777$; *O. spectabilis*: $\chi^2 = 4.79$, $p < 0.05$, $\beta_1 = 2.520$; *Q. multiflora*: $\chi^2 = 4.87$, $p < 0.05$, $\beta_1 = 0.941$; *S. polyphyllum*: $\chi^2 = 5.45$, $p < 0.05$, $\beta_1 = 3.585$; Figure 1b).

We found differences in the probability of termite survival among plant species 5 min ($\chi^2 = 12.83$, $p < 0.05$), 10 min ($\chi^2 = 14.99$, $p < 0.01$), and 15 min ($\chi^2 = 10.62$, $p < 0.05$) after starting the termite predation experiment (Figure 2). Termite survival curves for *Q. multiflora* and *O. spectabilis* at 5 min were different from those for *B. malifolia*, while the curves for *L. pacari* and *S. polyphyllum* were similar to those for *B. malifolia*, *Q. multiflora*, and *O. spectabilis* (Figure 2). At 5 min, we observed that 50% of all termites were preyed upon by *C. crassus* in *Q. multiflora*, 40% in *O. spectabilis*, 35% in *S. polyphyllum*, 20% in *L. pacari*, and 5% in

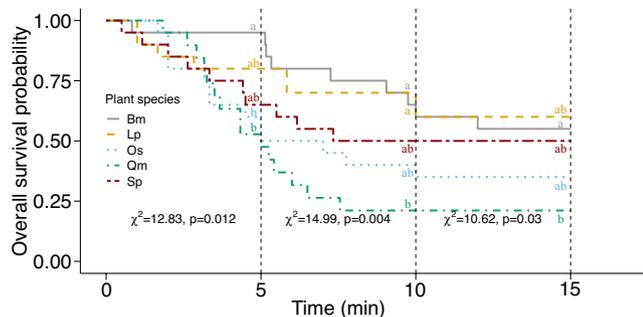


FIGURE 2 Variation in herbivore (termite) survival probability among five extrafloral nectary-bearing plant species attended by *Camponotus crassus* ants at 5 min, 10 min, and 15 min after termite addition. Vertical dashed lines represent the time of analyses. Differences among survival curves were tested with Weibull distribution and G-rho family followed by Log-Rank test (lowercase letter at each time of evaluation: 5 min, 10 min, and 15 min; $p < 0.05$). Bm—*Banisteriopsis malifolia*, Lp—*Lafoesia pacari*, Os—*Ouratea spectabilis*, Qm—*Qualea multiflora*, and Sp—*Stryphnodendron polyphyllum*

B. malifolia. At 10 min, we observed differences in the termite survival probability among *Q. multiflora* and other two species, *B. malifolia* and *L. pacari* (Figure 2). *Ouratea spectabilis* and *S. polyphyllum* presented similar curves to *B. malifolia*, *L. pacari*, and *Q. multiflora*. At 10 min, *Q. multiflora* (75%), *O. spectabilis* (60%), and *S. polyphyllum* (50%) had 50% or more predations of the termites. Finally, at 15 min termite survival probability for *Q. multiflora* was different from that for *B. malifolia* (Figure 2). The other three species had a survival probability similar to *Q. multiflora* and *B. malifolia*. At 15 min, *Q. multiflora* had 75% of termite predation, *O. spectabilis* had 65%, *S. polyphyllum* had 50%, and *B. malifolia* and *L. pacari* had 45% and 40%, respectively.

We observed differences in the protective effectiveness (PE) of *C. crassus* ants among plant species at 5 min (GLM: $\chi^2 = 26.004$, $p < 0.001$, McFadden *pseudo R*² = 0.014; Figure 3a,b), 10 min (GLM: $\chi^2 = 37.207$, $p < 0.001$, McFadden *pseudo R*² = 0.017; Figure 3c,d), and 15 min (GLM: $\chi^2 = 18.205$, $p < 0.01$, McFadden *pseudo R*² = 0.015; Figure 3e,f). At 5 min, the PE of *C. crassus* ants for *Q. multiflora* was 2.83 and 2.5 times greater than for *B. malifolia* and *L. pacari* (Figure 3b), respectively. The PE for *O. spectabilis* and *S. polyphyllum* was similar to that for *Q. multiflora*, *B. malifolia*, and *L. pacari* (Figure 3b). At 10 min, the PE of *C. crassus* ants for *Q. multiflora* was 2.92, 3.08, 1.81, and 1.54 greater than for *B. malifolia*, *L. pacari*, *O. spectabilis*, and *S. polyphyllum* (Figure 3d), respectively. At 15 min, the PE of *C. crassus* ants for *Q. multiflora* was 2.48, 2.68, and 2.17 greater than for *B. malifolia*, *L. pacari*, and *S. polyphyllum*, respectively, but did not differ from *O. spectabilis* (Figure 3f). The PE for *B. malifolia*, *L. pacari*, *O. spectabilis*, and *S. polyphyllum* did not significantly differ between themselves (Figure 3f).

4 | DISCUSSION

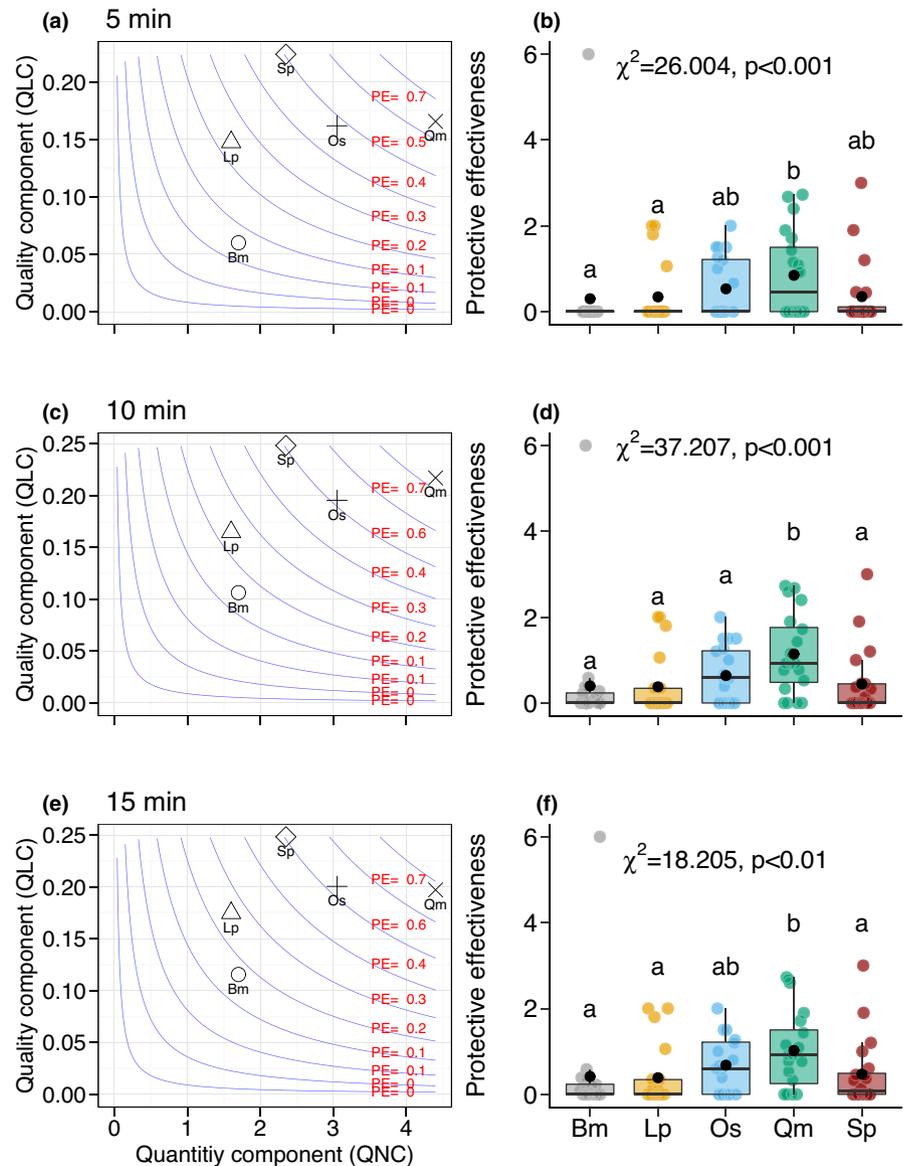
Our results showed that ant abundance markedly varied among the five EFN-bearing plant species. In particular, we found that the

abundance of *C. crassus* ants was greater in *Q. multiflora* and *O. spectabilis*: The former had the highest volumes and sugar concentrations of extrafloral nectar, and the latter the second highest volume of nectar (Table 1). Since extrafloral nectar is fundamental for larval growth, ovary development, and egg production in adults (Byk & Del-Claro, 2011; Nation, 2015), higher volume and sugar concentration in the EFNs should attract more ant individuals. In agreement with our results, Bixenmann et al. (2011) showed that increases in sugar concentration of nectar significantly enhanced ant visitation to leaf surfaces in seven species of *Inga*. Likewise, Pacelhe et al. (2019) found that ant recruitment was higher in *Vochysia elliptica* plants with artificial EFNs including higher concentrations of sugar and amino acids than in less nutritious artificial EFNs. As expected, we also found that greater ant abundance resulted in a higher probability of herbivore (termite) finding by ants for all plant species. Similarly, Apple and Feener (2001) found that *Passiflora* plant species with the largest and most abundant EFNs attracted more ants, resulting in higher rates of discovery of termite baits. Although presenting a low sugar concentration (Table 1), *O. spectabilis* present a high number of EFNs per individual (ES Calixto pers. obs.), which can influence ant abundance and protective effectiveness. Together, our findings and those by Apple and Feener (2001) are in accordance with the predator recruitment hypothesis, which posits that higher abundance of EFNs increases the local density of predatory ants, enhancing ant predatory effects on herbivores (Rosumek et al., 2009).

It is important to note that *Stryphnodendron polyphyllum* plants attracted fewer ants in comparison with the rest of plant species included in our study, even though it produces a large amount of nectar rich in carbohydrates. One potential explanation for this unexpected finding might be the architecture of the plant. This Fabaceae species bears EFNs at the base and apex of the petiole of each leaf. However, compared to the other plant species studied, *S. polyphyllum* has a much lower number of branches and leaves (ES Calixto. pers. obs) which likely reduced the total production of extrafloral nectar per plant, and consequently ant abundance.

Our results also suggest that ant protective effectiveness varied among five EFN-bearing plant species. Again, we found that *C. crassus* ants showed the highest values of protective effectiveness in *Q. multiflora*, the plant species exhibiting higher volumes and sugar concentrations of extrafloral nectar. Aggressiveness is an intrinsic trait of many ants, but it can be modified when one ant species territorially dominates and harvests large amounts of energetic resources such as the extrafloral nectar (Davidson, 1998; Davidson et al., 2003). For instance, plant exudate-feeders (e.g., ants) exhibiting high dietary carbohydrate:protein ratios support high performances of foraging activities, defense of absolute territories, and production of defenses (e.g., nitrogen-free alarm) that increase ecological dominance (Davidson, 1997). Then, ants with high plant-exudates demand often exhibit a more aggressive patrolling activity on plants. *Camponotus crassus* has 84% of its food composed of extrafloral nectar (most part) and honeydew produced by hemipterans during the rainy season in the Brazilian savanna (Lange et al., 2019), showing a high dietary carbohydrate:protein ratio. In a recent study, we

FIGURE 3 Variation in protective effectiveness (PE) index of the *Camponotus crassus* ant in five extrafloral nectary-bearing plant species analyzed at 5 min (a, b), 10 min (c, d), and 15 min (e, f). In the left panels (a, c, e), isoclines inform the average protective effectiveness index through the combination of quantity (QNC) and quality (QLC) components for each plant species. QNC is average of the total abundance of ants, and QLC is the average of the multiplication of the inverse of the time spent by ants to find the surrogate herbivore by the percentage of termites preyed by an ant. PE values in the left panels represent the protective effectiveness index. In the right panels (b, d, f), different letters indicate significant differences ($p < 0.05$) among plant species after GLM analysis, and black dots represent the mean value. Bm—*Banisteriopsis malifolia*, Lp—*Lafoensia pacari*, Os—*Ouratea spectabilis*, Qm—*Qualea multiflora*, and Sp—*Stryphnodendron polyphyllum*



found that herbivory pressure is higher during the rainy season and that EFN-bearing plants from Cerrado synchronized the production of new leaves and the activity of EFNs, ultimately attracting more ants (Calixto, Novaes, et al., 2021). Therefore, it is plausible that the production of more carbohydrate-rich extrafloral nectar (especially during the rainy season) leads to a greater predatory activity and protective effectiveness of *C. crassus* ants in EFN-bearing plant species. In agreement with our findings, Pacelhe et al. (2019) found that the proportion of termites preyed upon by ants in *V. elliptica* plants was greater in artificial EFNs with higher concentrations of sugar and amino acids. Similarly, Fagundes et al. (2017) found that ant predatory activity and protective effectiveness were positively associated with sugar concentration of extrafloral nectar in ten different plant species growing in an area of Rupestrian Grasslands (Brazil). Finally, using different concentrations of artificial sugar solutions with amino acids, Blüthgen and Fiedler (2004) showed that many ant species preferred sugar solutions containing mixtures of amino acids over pure sugar solutions.

Previous studies have demonstrated that chemical composition of EFNs is fundamental for driving foliage-dwelling ant foraging (Blüthgen & Fiedler, 2004; Calixto, Lange, Bronstein, et al., 2021; Fagundes et al., 2017; Lange et al., 2017; Pacelhe et al., 2019). For example, using artificial EFNs in *Vachellia constricta* (Fabaceae), Flores-Flores et al. (2018) showed that ant protective effectiveness changes according to extrafloral nectar sugar composition, in which carbohydrate-rich artificial nectaries had the highest ant protective performance. Further studies in our system should thus measure the chemical composition of nectar to make stronger generalizations, considering different ecological and evolution traits. In addition to chemical composition of EFNs, ant foraging patterns might drastically vary depending on plant tissues where EFNs are located (Calixto, Lange, Bronstein, et al., 2021). For instance, in a recent study (Calixto, Lange, Bronstein, et al., 2021) we found that extrafloral nectar volume and calorie content, as well as ant abundance, in *Q. multiflora* were higher in EFNs of reproductive tissues (inflorescences) compared to EFNs

of vegetative tissues (leaves) both before and after simulated herbivory, consistent with the predictions of the Optimal Defense Theory (McKey, 1974; Rhoades, 1979). In addition, sympatric EFN-bearing plant species might face the same herbivory pressure, but invest differently in ant-related protection (see Baker-Méio & Marquis, 2012). In this case, due to the phylogenetic distance between EFN-bearing plant species (different families) and because of differences in the assemblage of herbivores, plants should invest different amounts of resources in extrafloral nectar production. For instance, Raupp et al. (2020) showed that different types of foliar damage in *Qualea parviflora* lead to different extrafloral nectar production, ultimately influencing ant aggressiveness.

Overall, our results suggest that variation in EFN traits (production and sugar concentration) can result in plant species specificity of defensive behavior of a dominant foliage-dwelling ant in the Brazilian savanna. In order to get a better understanding about the specificity of ant-plant mutualistic interactions mediated by EFNs, further studies should address (i) how extrafloral nectar composition varies among a wider array of EFN-bearing Cerrado plant species; (ii) whether sugar concentration and composition of extrafloral nectar differ between different plant tissues (e.g., vegetative and reproductive organs), ultimately influencing ant protective behavior ("Optimal Defense Theory"; Calixto, Lange, Bronstein, et al., 2021); (iii) how the defensive behavior of the whole ant community (i.e., other less dominant ant species) varies among plant species; and (iv) how other traits (e.g., length of the period of EFN activity, direct chemical defenses such as phenolic compounds or terpenoids; ant nest distance) could potentially influence ant-plant protection interaction mediated by EFNs in the Cerrado.

ACKNOWLEDGEMENTS

We thank Clube de Caça e Pesca Itororó de Uberlândia for providing the study area, Melina Galdiano for helping with data collection, and four anonymous reviewers for their helpful comments on the manuscript. This study was financed in part by "Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001 (ESC), and by CNPq and FAPEMIG (KDC).

CONFLICT OF INTEREST

No potential conflict of interest was reported by the authors.

AUTHOR CONTRIBUTIONS

ESC, DL, and KDC involved in conceptualization; ESC involved in formal analysis; ESC involved in investigation; –ESC, DL, and KDC involved in methodology; DL, KDC involved in supervision; ESC, DL, XM, and KDC involved in visualization; ESC involved in writing the original draft preparation; ESC, DL, XM, and KDC involved in writing, reviewing, and editing.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad Digital Repository at <https://doi.org/10.5061/dryad.rxwdb rv8f> (Calixto et al., 2021).

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How to cite this article: Calixto, E. S., Lange, D., Moreira, X., & Del-Claro, K. (2021). Plant species specificity of ant-plant mutualistic interactions: Differential predation of termites by *Camponotus crassus* on five species of extrafloral nectaries plants. *Biotropica*, 53, 1406–1414. <https://doi.org/10.1111/btp.12991>