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Evaluating community effects of a Keystone Ant, *Azteca sericeasur*, on *Inga micheliana* leaf litter decomposition in a shaded coffee agro-ecosystem

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Abstract

Our research examined the effect of *Azteca sericeasur*, a keystone arboreal ant, on the decomposition of leaf litter of the shade tree, *Inga micheliana*, in coffee agro-ecosystems. This interaction is important in understanding spatial heterogeneity in decomposition. We hypothesized that *A. sericeasur* could affect leaf litter decomposition by excluding other ants, which could release decomposers, like collembolans, from predation pressure. Determining the relative strengths of these interactions can illuminate the importance of *A. sericeasur* in decomposition and nutrient cycling processes. We assessed the ant and arthropod communities surrounding 10 pairs of trees, where each pair included one shade tree with an established *A. sericeasur* nest. Tuna baits were used in conjunction with pitfall traps to assess the ant and arthropod community, and litterbags with *I. micheliana* leaf litter were used to assess rates of decomposition. The species richness of ants did not change in proximity to *A. sericeasur* nests, though the ant communities were distinct. Abundance of Collembola and community composition of other invertebrates did not change in the presence of *A. sericeasur* nests, and there were no differences in leaf litter decomposition rates. This contradicts past studies that suggest *A. sericeasur* reduces ant species richness in its territory. We suggest that other ants may avoid *A. sericeasur* by moving within and beneath the leaf litter. Our results indicate that there is no net effect of *A. sericeasur* on leaf litter decomposition.

KEYWORDS

agro-ecosystems, Chiapas Mexico, coffee agro-ecosystems, community assembly, ecosystem function, keystone species

1 | INTRODUCTION

The activity of animals can have important impacts on decomposition dynamics, with accelerating or decelerating effects (Gessner et al., 2010; Hättenschwiler, Tiunov, & Scheu, 2005). Animals impose important controls on terrestrial decomposition, along with climate, litter chemistry, and soil properties (Aerts, 1997; Swift, Heal, & Anderson, 1979). The relative importance of each can vary based on context and scale (Aerts, 1997; Prescott, 2010; Zhang, Hui, Luo, & Zhou, 2008). Lavelle, Blanchart, Martin, Martin, and Spain (1993) organize the factors with climate first, followed by soil properties, litter chemistry and quality, and lastly, animal activity.

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Though lowest on the proposed hierarchy and highly context dependent, animal activity can have important impacts on decomposition dynamics.

Several reviews detail the ways in which predators and herbivores might influence nutrient dynamics directly and indirectly, across timescales, and in both accelerating and decelerating fashions (Hunter, Reynolds, Hall, & Frost, 2012; Schmitz, Hawlena, & Trussell, 2010; Wardle, Bonner, & Barker, 2002). Direct effects include contributions to the detrital pool by way of cadavers, feces, and urine (Carter, Yellowlees, & Tibbett, 2007) or alteration of the detrital pool where herbivores induce changes in plant tissue or convert that tissue to more labile forms, like frass or insect body tissue (Schmitz et al., 2010, Hunter 2016). Indirectly, predators can mediate nutrient dynamics by altering the distribution, composition, abundance, and behavior of herbivores (Hawlena, Strickland, Bradford, & Schmitz, 2012; Hines & Gessner, 2012). This has been shown experimentally when exclusion of spiders increased Collembola density and, in turn, decomposition rates (Lawrence & Wise, 2000). Collembola and other grazers can increase microbial biomass which, consequently, accelerates decomposition rates (Hanlon & Anderson, 1979; Seastedt, 1984; Yang, Yang, Warren, & Chen, 2012). Schmitz, Beckerman, and O'Brien (1997) provide a classical example of top-down control where differing hunting strategies by predatory spiders in old fields alter the behavior of the dominant herbivore, a grasshopper. This interaction results in a distinct change in primary production and cascading effects on carbon lability and nitrogen mineralization in the old field system (Schmitz, 2008).

Litter-dwelling arthropods have been found to accelerate decomposition in some cases (Attignon et al., 2004, Hattenschwiler and Gasser 2005, Del Toro, Ribbons, & Ellison, 2015), while in others they decelerate it (Hunter, Adl, Pringle, & Coleman, 2003) or have no net effect (Gonzalez and Seastedt 2001), depending on which of the potential pathways is dominant. Predicting the effects of litter-dwelling arthropod trophic dynamics on decomposition is particularly challenging in tropical systems where leaf litter and litter communities are spatially and temporally heterogeneous (Kaspari & Yanoviak, 2009). Ants (Hymenoptera: Formicidae) may play a key role in determining litter decomposition dynamics in tropical systems (Clay, Lucas, Kaspari, & Kay, 2013; McGlynn & Poirson, 2012). In a mesocosm experiment, local biomass of ants was the primary factor regulating decomposition, exceeding the relative importance of soil chemistry where ants were present (McGlynn & Poirson, 2012). In addition to heterogeneity in abundance and richness, ants also exhibit a range of foraging strategies, predating at varying trophic levels (Blüthgen, Gebauer, & Fiedler, 2003; Tillberg, McCarthy, Dolezal, & Suarez, 2006; Platner et al., 2012; Roeder & Kaspari, 2017). Thus, effects of ants on decomposition may depend strongly on the community context in which they are embedded.

The keystone ant species, *Azteca sericeasur* (formerly identified at this site as *Azteca instabilis* [Philpott, Perfecto, Vandermeer, & Uno, 2009, Mathis, Philpott, & Moreira, 2011, Li, Vandermeer, & Perfecto, 2016]), provides a useful system for studying the impacts of arthropods omnivores on decomposition dynamics. While *A. sericeasur* nests in shade trees, it has a hemipteran mutualist, *Coccus viridis* (coffee green scale), on nearby coffee bushes, which it defends vigorously (Hsieh, 2015). The aggressive nature of *A. sericeasur* can exclude other ant species (Ennis, 2010) and other arthropods (Vannette, Bichier, & Philpott, 2017). *A. sericeasur* is a keystone species with a proven capacity to alter community composition via competitive exclusion and predatory effects (Vandermeer, Perfecto, & Philpott, 2010; Perfecto et al., 2014), and we expected that these effects could have important implications for leaf litter decomposition.

Here, we assess the effects of *A. sericeasur* on the litter-dwelling community surrounding its nest. We sought to investigate the indirect effects of *A. sericeasur*, as a keystone omnivore, on decomposition as mediated by its impact on ground-dwelling ants and the litter invertebrate community, including Collembola, which are important decomposers (Yang et al., 2012). We hypothesized a net positive effect of *A. sericeasur* on decomposition processes (Figure 1). We predicted that this net positive effect would act through the following causal pathway:

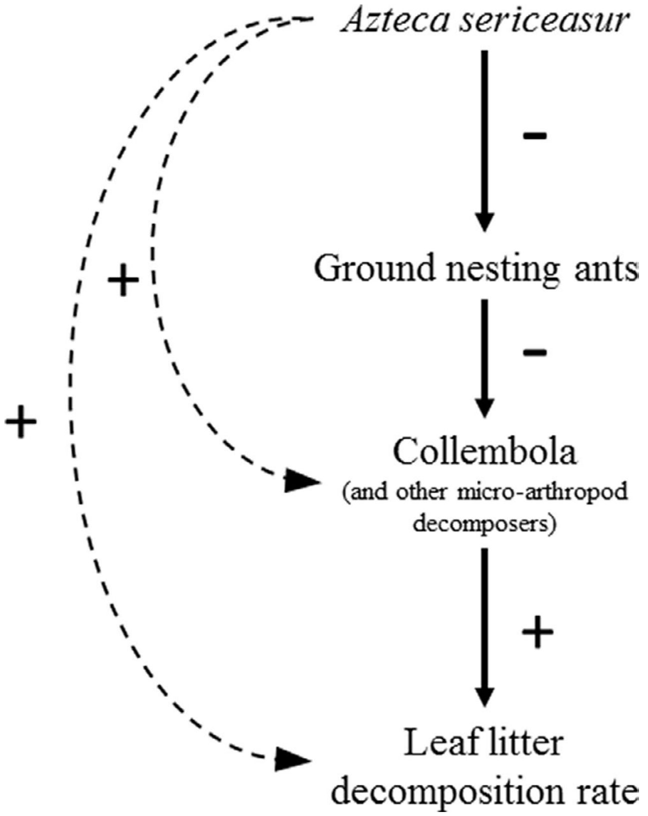

FIGURE 1 Model illustrating hypotheses. We expect *A. sericeasur* will reduce the diversity of ground-nesting ant species, due to their aggressive nature, which would release Collembola, a micro-invertebrate decomposer, from predation pressure and potentially increase leaf litter decomposition. Thus, we predict *A. sericeasur* will have a net positive effect on leaf litter decomposition rate, as mediated through ground-nesting ants

A *A. sericeasur* presence would decrease the species richness of ground-dwelling ants within close range of their nests, due to their aggressive exclusion of heterospecific ants.

B Lower species richness and abundance of ground-nesting ants would be associated with higher collembolan abundance, as several important ground-nesting ant species (including *Pheidole* spp.) are predators of Collembola.

C An increase in Collembola, and possibly other decomposers, would lead to increased mass loss in *I. micheliana* leaf litter since Collembola are important leaf litter detritivores.

2 | METHODS

2.1 | Study system

Azteca sericeasur has been well studied in coffee agro-ecosystems, where it nests in mid-canopy trees (Philpott, 2010). *Azteca sericeasur* (Hymenoptera: Formicidae: Dolichoderinae) is found in wet forests, and mature colonies can be polydomous (Longino, 2007). *Azteca sericeasur* has a mutualistic relationship with *Coccus viridis*, the coffee green scale. As is often the case in ant–hemipteran mutualisms, the ants defend the scale and feed on the sugary honeydew excreted by the scale. *Azteca sericeasur* provides defense from predators of the green coffee scale (Hsieh, 2015) and facilitates a faster growth rate of scale populations (Jha, Allen, Liere, Perfecto, & Vandermeer, 2012). *Azteca sericeasur* is omnivorous, relying on the honeydew from *C. viridis*, sugar from extrafloral nectaries and arthropod prey (Livingston, White, & Kratz, 2008; Philpott & Armbrecht, 2006). They exclude other ants (Ennis, 2010), alter the ant community (Philpott, 2010), exclude flying insects (Vannette et al., 2017), and lower the total abundance of arthropods on coffee plants around their nests (Vandermeer, Perfecto, Nuñez, Phillpott, & Ballinas, 2002). Further, *A. sericeasur* can serve as biocontrol, reducing the number of coffee berry borers and other pests on defended plants (Gonthier, Ennis, Philpott, Vandermeer, & Perfecto, 2013; Morris, Vandermeer, & Perfecto, 2015).

Previous research has demonstrated direct effects of ants in the *Azteca* genus on decomposition, as mediated by the inputs of refuse, including cadavers, feces, urine, and pieces of carton nest (Clay et al., 2013). However, the *Azteca* species studied by Clay et al. is known for building large carton nests, whereas *A. sericeasur*, the species of focus here, only occasionally builds carton nests and more typically nests in the lower trunks of live and dead shade trees (Livingston et al., 2008; Philpott, 2005).

We focused on the most common species of shade tree in the region, *Inga micheliana*, where nests are frequently found (Li et al., 2016). Trees in the *Inga* genus are ubiquitous as shade trees throughout coffee farms in the region, in part due to their ability to fix nitrogen (Grossman et al., 2006). At our study site, trees in the *Inga* genus make up more than half of all shade trees (Philpott & Bichier, 2012). Nitrogen fixation—especially in young *Inga* trees—has been found to be relatively low, and advantages for weed control have been modest (Romero-Alvarado et al., 2002, Grossman et al., 2006). Nonetheless, *Inga* spp. remain a common choice due to these perceived advantages (Romero-Alvarado et al., 2002). In coffee systems, *I. micheliana* can host *Octolecaium* sp. scale and have extrafloral nectaries (Livingston et al., 2008).

2.2 | Study site

This study was conducted at *Finca Irlanda*, a 300-ha. organic shaded coffee farm in the Soconusco region of Chiapas, Mexico. Altitude ranges from 900 to 1,200 m a. s. l. at the site, and mean annual rainfall is approximately 4500mm (Li et al., 2016). The region has two distinct seasons: a rainy season from May through October and a dry season from November through April. Community sampling took place in June and July of 2016, during the rainy season. Litterbags were in the field for one year, from July 2016 until July 2017.

Sampling was conducted at 10 locations, each of which included a pair of sites ($n = 20$ sites) oriented around a focal *I. micheliana* shade tree. One site in each pair had an *A. sericeasur* nest that had been active for at least 2 years. The other site in the pair, the control, had not supported a nest during the previous 3 years. The paired sites were 30–100 m apart (see supplementary Figure 1). Sampling took place in an area approximately 25 m^2, as described in detail below. There were no other *I. micheliana* trees in the sampling area, though there were coffee plants. Steep slopes and trees near pathways were avoided. *Azteca sericeasur* does not exhibit a strong affinity for nesting in particular shade tree species, so the location of the nests is correlated with the shade tree species abundance (Livingston et al., 2008). In all of our sites, *A. sericeasur* nests were located within the trunk of the tree; none had a visible carton.

2.3 | Sampling methods

Ant baiting was carried out at each site, around the focal tree, to determine the ant community. Four transects with 8 baits each, extending in each cardinal direction, were placed at each tree for a total of 32 baits per site. Baits were placed at 0.5 m increments from the base of the focal tree to 2.5 m away and at 1 m increments from 2.5 m to 4.5 m from the base of the focal tree. Thus, baits were sampled at 0, 0.5, 1, 1.5, 2, 2.5, 3.5, and 4.5 m from the focal tree (see supplementary Figure 2). A pinch of canned tuna was placed as bait on a cleared patch of soil and allowed to sit for 20 min, so that ants could locate and recruit to the bait. Tuna baiting is a widely used method for assessing the ant community, including in coffee agro-ecosystems (Philpott, Perfecto, & Vandermeer, 2006). Ants at all baits were identified to species or morpho-species. Most ants were identified in the field, but in cases where an identification could not be made in the field, individual ants were collected and identified at the field station. Guides from published taxonomy resources were used first to make identifications (Bolton, 1994, Fernandez 2003), followed by

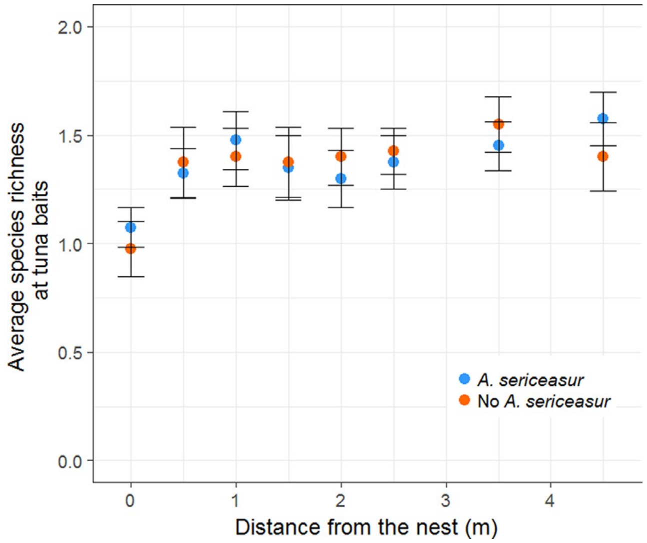

FIGURE 2 Average species richness at tuna baits. Error bars represent standard error

"antwiki.org." Reference specimens were collected when baiting to ensure identifications were standardized between baiting and pitfall samples.

Pitfall traps were used one week after baiting. Four traps were used at each site—two within the activity radius of *A. sericeasur* and two outside of their radius. The traps within the radius were placed 0.5 m from the focal tree, a radius at which *A. sericeasur* was recorded at all trees with nests. The traps outside the radius of *A. sericeasur* were placed 2 m from the focal tree, where no *A. sericeasur* was observed at the tuna baits (see supplementary Figure 2). Pitfall traps were buried flush with the ground and shaded by a larger lid to prevent falling debris or rain from entering. Traps were left closed for 24 hr after burial to reduce disturbance effects. Once opened, the traps were left open for 48 hr before re-collection. We used this ant data to complement the data from the tuna baits, since not all ant species are attracted to tuna (Philpott et al., 2006) and competition can reduce the co-occurrence of ant species at baits where competitively dominant species are found (Perfecto, 1994). The ants in the pitfall traps were identified to species or morpho-species (supplementary Table 1). We used guides (Bolton, 1994, Fernandez 2003), as well as "antwiki.org" and the reference samples taken from the tuna baiting to ensure morpho-species identifications remained consistent. The ants collected were kept to create a reference collection, which is located at the University of Michigan (Ann Arbor, MI, USA). All other invertebrates in the pitfall traps were stored in ethanol and identified to order or family.

Litterbags were assembled using a homogenized batch of recently senesced *I. micheliana* leaves collected from the field site and dried in an oven at 50°C to a constant weight. Five-millimeter fiberglass mesh (Saint-Gorbain ADFORS, www.adfors.com) was used, which allows most decomposer invertebrates to access the leaf material (Bradford, Tordoff, Eggers, Jones, & Newington, 2002). A total of 8 litterbags were placed at each site, at a point 1 m from the focal tree. The distance of 1 m was chosen because that was within the range of *A. sericeasur* at each of our focal trees with a nest. Litterbags were collected from each site after 2 weeks, 1 month, 2, 4, 6, 8, 10, and 12 months. This time frame is appropriate in the tropics, as climatic conditions result in most leaf litter decomposing within the year (Powers et al., 2009). Collected litterbags were dried and weighed (± 0.2 g, using American Weigh Scale [Cumming, Georgia] 1 kg scale) to determine mass loss.

2.4 | Statistical methods

We used the non-parametric Wilcoxon signed-rank test to compare species richness of ants at the tuna baits, which was appropriate because a) the control and treatment sites were paired and b) the data were non-normal, with outliers, which violate assumptions of parametric tests. A one-sided test was used to test the hypothesis that there would be a lower species richness of ants at the sites with *A. sericeasur* nests. We also created a linear mixed-effects model using the "lmer" function within "*lmerTest*" package in R (Kuznetsova, Brockhoff, & Christensen, 2017). This allowed us to test for differences in species richness by treatment while controlling for variation in local richness between pairs by using "pair" as a random effect.

We estimated species richness with rarefaction curves created with the "*vegan*" package in R and used the "rarefaction" method (Oksanen et al., 2007). We used the "adonis" function in the "*vegan*" package to compare communities (Oksanen et al., 2007). This is functionally equivalent to permutational multivariate analysis of variance (PERMANOVA). We calculated distances based on Bray–Curtis, which is appropriate for our count data, and ran 1,000 permutations. This was repeated for the ant community data from the tuna baits and the pitfall traps. "Adonis" provides R^2 as an output (rather than pseudo-*F* values), which indicates the strength of the relationship. We pooled data at the level of the tree to avoid pseudo-replication, but for the pitfall traps, we also looked at the effect of distance at each tree ($n = 40$).

The "adonis" function was used to look for differences in the arthropod community composition in the pitfall traps, and non-metric multidimensional scaling (NMDS) was used to visualize differences in these communities. NMDS was computed using the "metaMDS" function from "*vegan*" in R (Oksanen et al., 2007) with the Bray–Curtis dissimilarity index and with three dimensions ($k = 3$) to reduce our stress values. The matrix was computed using the arthropod data identified to order or family and without any environmental factors. We carried out this analysis with data pooled by tree and distance and, to be conservative, by tree. We used the non-parametric Kruskal–Wallis test to assess differences in collembolan abundance in the pitfall traps because the residuals were not normally distributed, violating a key assumption of parametric tests.

The decay constant (k) was used to assess decomposition rates and compared between treatments, as is standard in the decomposition literature (Olsen 1963, Melillo, Aber, & Muratore, 1982). The decay constant, k, comes from the exponential decay equation ($N_t = N_0 * e^{-k*t}$). We created a linear mixed-effects model using the "lmer" function within "*lmerTest*" package in R (Kuznetsova et al., 2017) to assess the effect of time, *A. sericeasur*, collembolan and other ants within the radius of *A. sericeasur* and the interaction of time and the presence of *A. sericeasur* on the decay constant, k. To correct for non-normal residuals, k was log-transformed. Site was included as a random effect to control for site-based correlation.

3 | RESULTS

Sites with *A. sericeasur* nests had an average species richness of 32 ground-dwelling ants, which was slightly greater than the 28 species found in sites without *A. sericeasur* nests. However, this difference was not statistically significant ($V = 13$, $p = .263$). The presence of *A. sericeasur* was not a significant predictor of species richness at the tuna baits ($\beta = 0.8$, $df = 9$, $p = .393$). On average, there were 1–1.5 species of ant at the tuna baits, regardless of the bait's distance from the focal tree (Figure 2). Estimated ant species richness from the pitfall traps was lower in the traps near to (0.5 m) *A. sericeasur* sites compared to traps placed far from (2 m) the nests, though all four treatments failed to reach an asymptote indicating we sampled a portion of the total ant community (Figure 3).

The ant community composition around *A. sericeasur* nests was distinct from the community composition at trees without *A. sericeasur* nests (tuna baits, $R^2 = .122$, $p = .003$; pitfalls, $R^2 = .06$, $p = .004$). Differences in the ant community composition at the pitfalls were not dependent on distance ($R^2 = .04$ $p = .09$), nor was there a strong interaction between distance and treatment ($R^2 = .03$, $p = .39$). Nevertheless, even after pooling traps across distances, the ant communities around focal trees with *A. sericeasur* were distinct from the communities around trees without *A. sericeasur* nests ($R^2 = .12$, $p = .01$). The community of ants sampled through tuna baits and pitfall traps is reported in Table S1.

Despite statistically distinct ant communities, there is not visual separation in the overall communities found in the pitfall traps (Figure 4). Here, the community, based on the pitfall trap samples, includes Diptera, Hymenoptera (divided into ants and non-ants), Arachnida, Coleoptera, Orthoptera, Isopoda, Hemiptera, Collembola, and all others (see Table S2). The stress value for our NMDS visualization was 0.163 indicating good representation. The community of organisms in the pitfall traps did not differ based on distance to the tree (adonis; $R^2 = .032$, $p = .29$) or presence of *A. sericeasur* ($R^2 = 0.024$, $p = .43$), and there was no interaction between distance and *A. sericeasur* ($R^2 = .03$, $p = .26$). Accordingly, there were also no differences in the overall community at the level of tree when pooling across distances ($R^2 = .04$, $p = .51$).

On average, there were 64 collembolans in the sample taken 0.5 m from a focal *A. sericeasur* tree and 63 collembolans at 2 m from focal *A. sericeasur* trees. Focal trees without *A. sericeasur* averaged 64 collembolans in 0.5 m samples and 74 collembolans at 2 m. These differences were not statistically significant (Kruskal–Wallis, chi-square = 0.254, $df = 3$, $p = .968$).

Only time was a significant predictor of the decay constant k in our model ($\beta = -0.01$, $df = 125.2$, $p < .001$). The presence of an *A. sericeasur* nest at the focal tree ($\beta = 0.005$, $df = 68.9$, $p = .975$), the abundance of non-*A. sericeasur* ants ($\beta = 0.0004$, $df = 12.8$, $p = .553$) and abundance of collembolan ($\beta = -0.0003$, $df = 14.2$, $p = .639$) within the range of *A. sericeasur*, and the interaction term between *A. sericeasur* and time ($\beta = 0.006$, $df = 124.7$, $p = .483$) were all non-significant in our model.

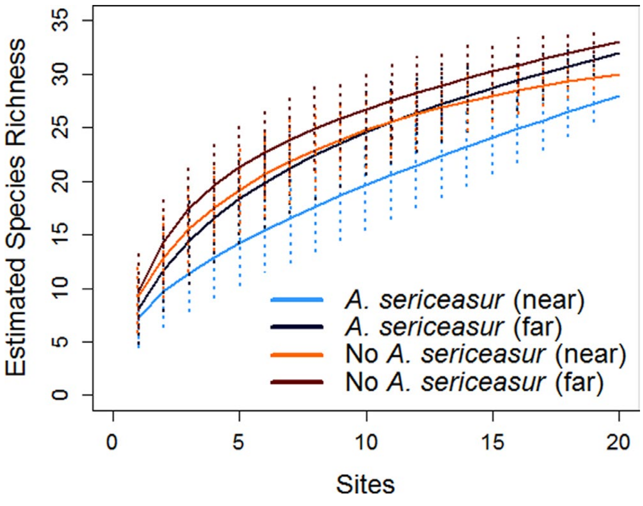

FIGURE 3 Rarefaction curves for the four treatments (with *A. sericeasur* and without *A. sericeasur*, at distances near [0.5m] and far [2m] from the tree). Dashed lines indicate a 95% confidence interval

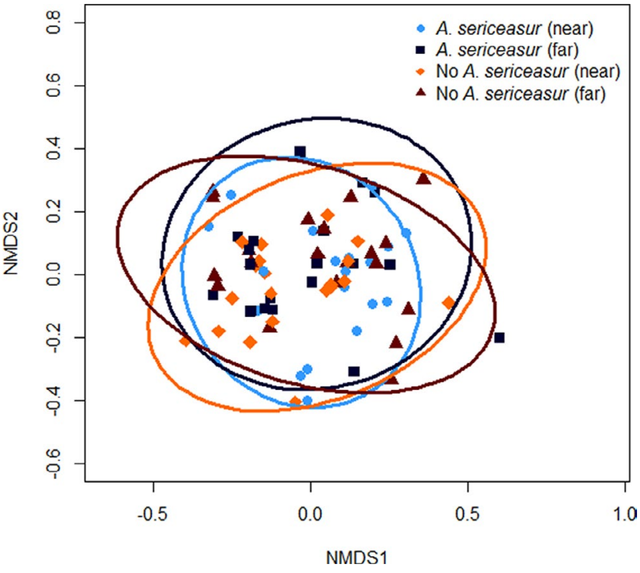

FIGURE 4 NMDS plot of pitfall traps at sites with *A. sericeasur* nests (A) and without nests (N). Traps were placed 0.5 m from the tree (near) and 2 m from the tree (far) to compare communities within and outside the range of *A. sericeasur*. Ellipses represent 95% confidence intervals, and the final stress value was 0.163

4 | DISCUSSION

Our findings suggest that *A. sericeasur* may alter ant community composition and influence the litter community through higher-order interactions, rather than simple exclusion of other ants. We found weaker-than-expected effects of *A. sericeasur* on the invertebrate community around their nests and no effect of *A. sericeasur* on leaf litter decomposition.

Our finding that leaf litter ant species richness was unchanged in close proximity to *A. sericeasur* nests contradicts most existing research that suggests *A. sericeasur* excludes other ants from the areas immediately surrounding their nests (Ennis, 2010; Philpott, 2010). However, not all studies have found an effect of *A. sericeasur* on the ant community. Philpott et al. (2004) found that the presence of *A. sericeasur* decreased colonization rates of common twig-nesting ant species but had no effects on rare species.

The discrepancy between our results and results from other studies focusing on *A. sericeasur* could be due to a potential behavioral adaptation of non-dominant ants to avoid *A. sericeasur*. Previous studies have documented the effect of *A. sericeasur* on other insects that forage arboreally (Philpott, Maldonado, Vandermeer, & Perfecto, 2004; Vandermeer et al., 2002), rather than on the ground. Our focus was on the leaf litter layer, which is shown here to support other ant species within a small radius of *A. sericeasur* nests. Thus, the maintenance of leaf litter on the soil surface could support ant species richness, even where *A. sericeasur* is dominating arboreal ant communities. *Azteca sericeasur* is known to use twigs, leaf litter, and other detritus for pathways, nearly always avoiding walking on the soil. While never tested explicitly, to our knowledge, this behavioral preference is anecdotally supported and underscored by an increase in *A. sericeasur* foraging where connectivity is artificially augmented by ropes and bamboo (Jimenez-Soto, Morris, Letourneau, & Philpott, 2019). If *A. sericeasur* avoids walking on soil, other ant species that may otherwise forage arboreally may shift their behavior in the presence of *A. sericeasur* to avoid encounters. This higher-order interaction could be responsible for the community differences found in our study between sites with and without nests both at the baits and in the pitfall traps.

Alternatively, it may be that we found no effect of *A. sericeasur* on leaf litter ant richness because *A. sericeasur* foraging activity at the time of sampling—the rainy season—was focused on shade trees rather than on coffee bushes. *Inga micheliana* have extrafloral nectaries and host *Octolecanium* sp. helmet scale (Livingston et al., 2008), both of which provide alternative sources of sugar for *A. sericeasur*. Moreover, during the rainy season, when the study was conducted, *C. viridis* has reduced sugar content (Rivera-Salinas, Hajian-Forooshani, Jiménez-Soto, Cruz-Rodríguez, & Philpott, 2018), while extrafloral nectaries are more productive (Rico-Gray, García-Franco, Palacios-Rios, Íz-Castelazo, Parra-Tabla, & Navarro, 1998). Further, *C. viridis* occurs in lower densities around *I. micheliana* with *Octolecanium*, suggesting competition between the scale species and a preference of *A. sericeasur* for *Octolecaium* (Livingston et al., 2008). We did not monitor scale densities on the coffee bushes nor on the shade trees. A minimum level of ant activity was a pre-requisite for site selection, but it is not known where the ants were primarily foraging. If *A. sericeasur* was primarily foraging in the crown of *I. micheliana* at the time of the study, its effects on ground-dwelling ants would be reduced.

Seasonal dynamics of scale insects (both *Octolecanium* sp. and *C. viridis*) may alter the food sources available to *A. sericeasur*, but the dietary needs of *A. sericeasur* also change between seasons. Past research has suggested that *A. sericeasur* are not sugar limited at the start of the rainy season, as they have not shown a preference for high density *C. viridis* patches (Rivera-Salinas et al., 2018). However, despite the complications that distinct seasonality presents, the timing of our sampling is consistent with past work on *A. sericeasur* where they have been found to exclude other ant species (Ennis, 2010, Rivera-Salinas, 2019).

Previously, *A. sericeasur* has been assumed to be a dominant keystone species. These results do not support this conclusion, in regard to brown food web or detrital dynamics, where the invertebrate community appears to be unchanged by the presence of *A. sericeasur*. Other ants, including those in the *Pheidole* genus, which are primarily predators, are more likely to have a strong effect on the brown food web (Shukla, Singh, Rastogi, & Agarwal, 2013; Wilson, 2005). We did not find support for our hypothesis that *A. sericeasur* was excluding other ant species and suggest that the presence of *A. sericeasur* might even be driving other ant species to spend more time within the leaf litter layer. Nonetheless, we find no evidence of an effect of *A. sericeasur* on the litter-dwelling community.

The lack of a net effect of *A. sericeasur* on decomposition is not unexpected, given the similarity in the detritivore communities around trees with and without *A. sericeasur* nests. Our study relied on site choice, rather than direct manipulation, to evaluate the effects of ants and litter-dwelling detritivores on decomposition. Because of the unexpectedly weak effects of *A. sericeasur* on ant and litter-dwelling detritivores, we could not disentangle the effects of ants and the effects of micro-arthropods. In a study conducted in Costa Rica, decomposition decreased where ants were excluded but micro-arthropods were allowed access to the litter, suggesting a cascade in which ants prey upon micro-arthropods that are grazing upon decomposer microbes (McGlynn & Poirson, 2012). Studies that use litterbags of varying mesh sizes to control access to the litter are needed, as are studies that directly manipulate abundances and community composition.

The results from this study suggest that top-down effects of predators on decomposition dynamics are weak in this system. However, we caution that these results may not be widely applicable and instead highlight the context dependency of such top-down effects. In this case, *A. sericeasur* did not influence decomposition dynamics nor did it appear to influence the invertebrate community or abundance of other ants, but it did change the community composition of ants. Further research is needed to determine whether this is due to temporally and spatially specific constraints on *A. sericeasur* dominance or resilience in the decomposer community.

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4qrfj6q7k (Schmitt, Aponte-Rolón, & Perfecto, 2020).

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SUPPORTING INFORMATION

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