



Weaver Ants Provide Ecosystem Services to Tropical Tree Crops

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Generalist predators bring a complex mix of beneficial and harmful effects to agroecosystems. When these predators feed on herbivorous pests, biological control is improved with the potential to increase crop yield. However, generalists often feed on predators, pollinators, and plants, which might worsen pest outbreaks and reduce fruit set. For example, weaver ants (*Oecophylla smaragdina*) are major predators of several key, economically-damaging pest insects of tropical fruit and nut crops. Yet the ants also attack other predatory arthropods and important pollinators, while tending trophobiont honeydew producers like mealybugs (Pseudococcidae) that are themselves pests. Finally, ants will supplement their diet with sugars from floral and extrafloral nectaries, a form of plant feeding that presumably carries a physiological cost to the plant. Here, across previously-published experimental studies that compared treatments where ants were present vs. excluded, we summarize the effects of weaver ants on beneficial and pest insects and tree-crop productivity. Our quantitative review revealed nearly ubiquitous benefits of *Oecophylla* ants for tropical agriculture. Treatments with ants present generally showed lower pest densities and damage from pest insects in the families Coreidae, Miridae, Pentatomidae, and Tephritidae. Pest reduction was seen on cacao (*Theobroma cacao*), cashew (*Anacardium occidentale*), and mango (*Mangifera indica*) trees. The single exception to these pest reductions occurred when ants facilitated the population growth of mealybugs and other honeydew producers. In general, we found that *Oecophylla* ants provided the valuable ecosystem service of natural pest control to a diversity of tropical tree crops. Despite the potential for the ants to harm other predators or pollinators, evidence for these ecosystem disservices was rare and other beneficial insects co-exist well with this group of ants. Our findings bolster the general finding that ant species that tend herbivores who are not themselves pests can provide broad-reaching benefits to plant productivity. More generally, our findings are consistent with the many cases where non-pest prey bolster densities of polyphagous predators with benefits for biological control despite some degree of plant feeding by the predators.

Keywords: *Oecophylla*, biocontrol, yield, generalists, predators, agroecosystems, ants

INTRODUCTION

Biological control agents can be broadly divided into specialists and generalists. Specialists have long been used as successful biological control agents, with part of their effectiveness lying in an ability to quickly reproduce and outnumber the relatively few prey/host species on which they feed (Snyder and Ives, 2001). The disadvantage of these predators' specificity, however, is that they provide little protection against the emergence of pest species other than the relatively narrow range of hosts/prey species that they attack (Symondson et al., 2002). In contrast, generalist predators can combat a suite of pests and this polyphagy allows them to remain in a field as various prey species become more or less common (Offenberg, 2015; Thurman et al., 2017). However, the same diverse feeding habits can lead to harmful attacks on predators and parasitoids (Snyder and Ives, 2001, 2003; Mathews et al., 2011; Ramesh et al., 2016) weakening biological control, or on pollinators (Dukas, 2005; Rodriguez-Girones et al., 2013; Yamasaki et al., 2016), decreasing fruit set (Abdulla et al., 2015, 2017; Anato et al., 2015, 2017). Furthermore, some broadly polyphagous generalists feed on the host plant in addition to arthropod prey (Eubanks and Denno, 1999; Bluthgen and Fiedler, 2002, 2004; Ingegno et al., 2011), and we must consider the potential direct crop damage caused by their plant-feeding.

Arboreal ants (Formicidae) present one class of generalist predators that supplements its diet with plant material. This can occur either when ants feed directly on host plant nectar, or indirectly while tending herbivorous insects that release sugars or other nutrients on which the ants feed (i.e., a trophobiotic relationship is in place) (Hölldobler and Wilson, 1990; Bluthgen and Fiedler, 2002; Bluthgen et al., 2004). An example of this trophobiosis is when aphids (Aphididae) produce a sugary honeydew secretion while feeding on a plant, which the ants can then consume. Stable food resources provided by the plant and/or trophobionts can then support relatively large ant colonies able to effectively antagonize and kill herbivore species that otherwise might damage the plant (Bluthgen and Fiedler, 2002; Davidson et al., 2003). Weaver ants (*Oecophylla* spp.) are recorded to harvest nectar from their host plant, while also "farming" trophobionts like soft scales (Coccidae) and mealybugs (Pseudococcidae) (Bluthgen and Fiedler, 2002). This is thought to make the ants highly territorial with large resident colonies unlikely to leave a site, and thus likely to heavily impact any herbivores attempting to colonize the host plant (Peng et al., 2002; Offenberg, 2015). In fact, weaver ants are the oldest documented form of biological control with records of *Oecophylla smaragdina* being conserved for natural pest control in 304 AD China (Way and Khoo, 1992).

Weaver ants have the potential to control agricultural pests across many tropical countries, as *Oecophylla smaragdina* (Fabricius) is found in Australia, India, and South-East Asia, and *Oecophylla longinoda* (Latrielle) in Sub-Saharan Africa (Vayssieres et al., 2015; Wetterer, 2017). *Oecophylla smaragdina* has been recorded to control over 50 pest species in eight different horticultural crops (Peng and Christian, 2004; Offenberg et al., 2013), while in sub-Saharan Africa its congener *O. longinoda* was observed consuming 48 arthropod species comprising 78.7%

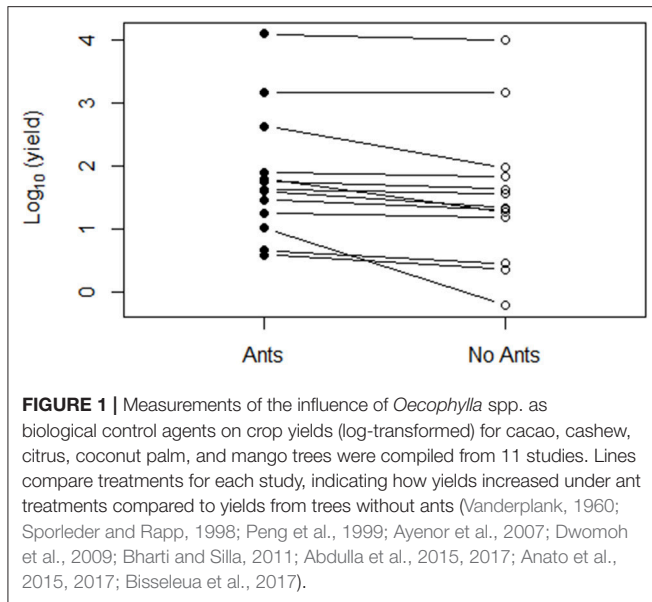
of all mango pests (Vayssieres et al., 2015). Previous reviews of *Oecophylla* spp. as biological control agents suggest that these ants successfully manage pests in some situations (Way and Khoo, 1992; Van Mele, 2008; Offenberg, 2015), with the potential to improve yields, although individual cases suggest harmful effects of the ants on other beneficial arthropods that could counterbalance these benefits (e.g., Delabie, 2001; Bluthgen et al., 2006). In order to determine when ant presence is generally improving crop production in the tropics, we need to carefully consider the relative strengths of these ant's helpful vs. harmful effects.

Here, we conduct a quantitative literature review of the potential for the weaver ants *Oecophylla smaragdina* and *O. longinoda* to control a diversity of pests and improve yields across a wide range of tropical tree fruit and nut crops. We first quantify the impact of *Oecophylla* spp. on crop yield, pest density and damage. We then supplement this analysis with case studies on how *Oecophylla* spp. feed on their host plant, harvest honeydew producers, and deter some predators, parasitoids and pollinators. Together, this generates a holistic assessment of the costs and benefits of using these ants as biocontrol agents. Insights from the case studies presented here help define the conditions when weaver ants provide ecosystem services vs. disservices. We also seek to provide a blueprint for when other ant species, and generalist biological control agents more broadly, might be expected to improve biological control based on their relationship to their host plant and resident harmful and beneficial arthropods.

MATERIALS AND METHODS

We began with a comprehensive literature search using Web of Science and "Oecophylla" as the search term. A total of 356 papers resulted from this search (last conducted March 2018), and all abstracts from these papers were reviewed to find 97 that considered the effects of *Oecophylla* spp. in agriculture. After reviewing the methods and data of these 97 articles, we identified 34 that (1) experimentally compared ant treatments that included either *O. smaragdina* or *O. longinoda* to a no-ant control treatment, and/or (2) reported changes in crop yield (11 of the 34 studies), pest numbers (8 of the 34 studies), and/or pest damage (15 of the 34 studies) under +ant and – ant treatments. These studies came from a range of crop systems with fourteen studies in mango, eight in cashew, four in mahogany, three in cacao, three in citrus, two in coconut palm, only one study each for palm oil and pongamia crops. We had hoped to find data reporting how ant manipulation impacted beneficial insects like predators and pollinators in agroecosystems, but these data were too sparsely studied for analysis. After extracting data from the studies, we then analyzed the pooled results of these papers according to their response variables (crop yield, pest density, or pest damage) by performing sign tests on how frequently ant treatments (ants and no ants) were shown to increase or decrease the aforementioned response variables.

Additional studies located in the original literature search were then reviewed for case studies that investigated how weaver



ants interact with their host tree and arthropod community to provide possible mechanistic underpinnings for the patterns seen in the quantitative literature review.

RESULTS

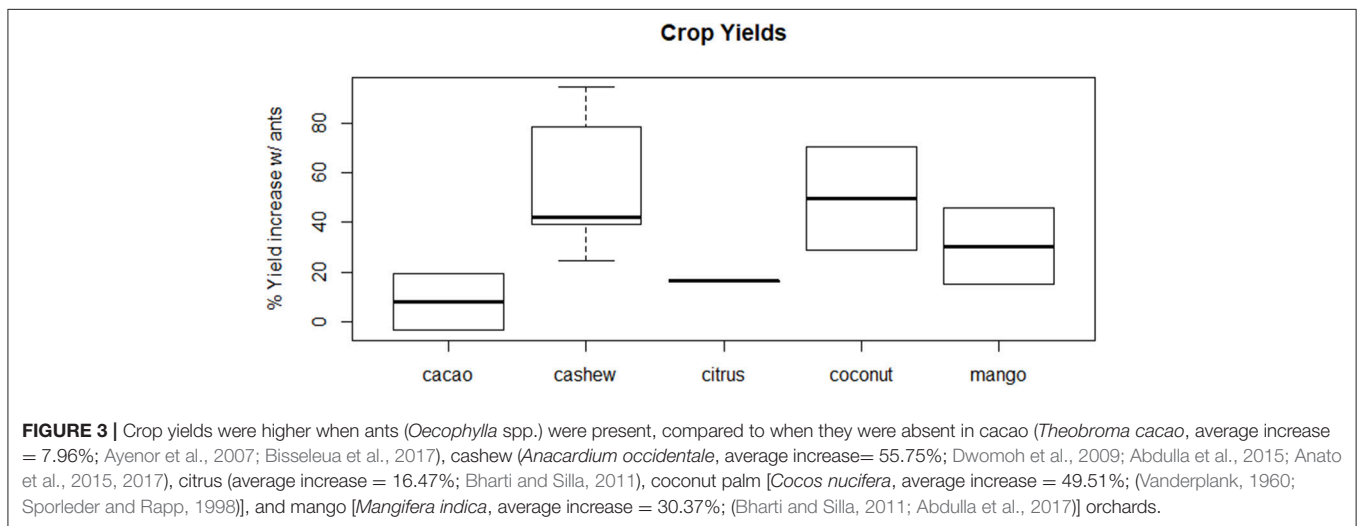
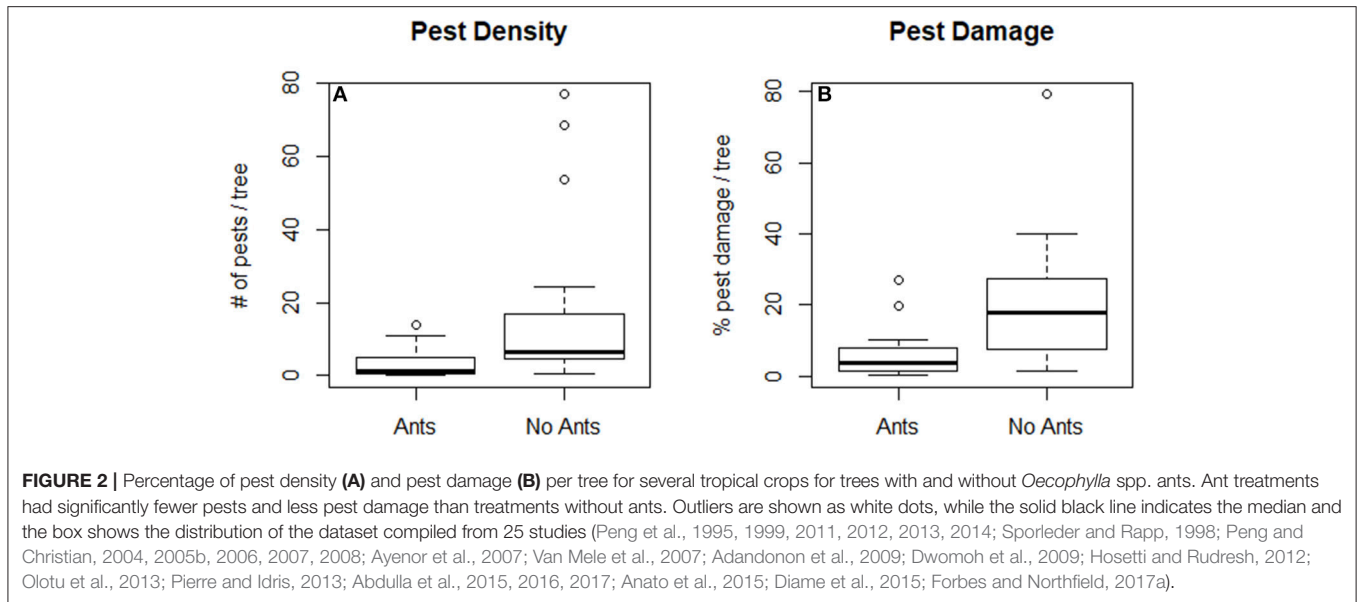
Our quantitative literature review found that the weaver ants *O. smaragdina* and *O. longinoda* generally reduced pest density and damage when summed across crop and pest types (Figures 1, 2). Overall, ant presence in trees resulted in higher yields than were seen in trees where ants were experimentally excluded (sign test: 12/13, $p < 0.005$; Figure 1). There were lower pest densities in 13 out of 16 case studies (sign test: 13/16, $p < 0.05$; average = -13.94% pests; Figure 2A) and less pest damage in 18 out of 19 case studies (sign test: 18/19, $p < 0.0001$; average = -10.92%) (Figure 2B). Ants presence correlated with higher yields across five crop types, with average increases of 7.96% in cacao (*Theobroma cacao*), 55.75% in cashew (*Anacardium occidentale*), 16.47% in citrus, 49.51% in coconut palm (*Cocos nucifera*), and 30.37% in mango (*Mangifera indica*) orchards (Figure 3). Ants reduced pest density and/or damage for herbivores in seven insect families (Chrysomelidae, Coreidae, Curculionidae, Miridae, Pentatomidae, Tephritidae, and Thripidae) (Figures 4A,C). Reductions in pest damage and/or densities were seen in trees with ants compared to those without ants, across all crops for which these data were sufficient to be statistically analyzed, in cacao (*Theobroma cacao*), cashew (*Anacardium occidentale*), mango (*Mangifera indica*), and mahogany (*Khaya senegalensis*) (Figures 4B,D). These results were also consistent across the two ant species (Supplementary Figure 1).

In particular studies, the presence of ants significantly reduced pest densities of leaf-footed bugs (Coreidae; Peng et al., 1999; Dwomoh et al., 2009), mirid bugs (Miridae; Peng et al., 1999;

Ayenor et al., 2007; Dwomoh et al., 2009; Forbes and Northfield, 2017a), stink bugs (Pentatomidae; Peng et al., 1999; Hosetti and Rudresh, 2012) and fruit flies (Tephritidae; Van Mele et al., 2007; Adandonon et al., 2009; Migani et al., 2017) (Figure 4A). Particular studies reported reduced pest damage from weevils (Curculionidae; (Peng and Christian, 2007; Peng et al., 2014; Abdulla et al., 2016)), fruit flies (Peng and Christian, 2006; Diame et al., 2015; Abdulla et al., 2017), and mirid bugs (Peng et al., 1995, 2014; Peng and Christian, 2008; Olotu et al., 2013; Abdulla et al., 2015) in the presence of ants (Figure 4C). Most studies focused on heteropteran, weevil, or fruit fly pests, with single studies focusing on density of leaf beetles (Chrysomelidae; average = -46.1% ; Forbes and Northfield, 2017a) and thrips (Thripidae; average = -80.74% ; Peng and Christian, 2004), and damage by snout moths (Pyralidae; average = -94.86% ; Peng et al., 2011, 2014). Interestingly, damage from thrips increased by 68.75% under ant treatments compared to the no ant control treatment in one cashew orchard study (Anato et al., 2015), which contrasts with other cases of reduced thrips density (Peng and Christian, 2004) and damage (Abdulla et al., 2015) by ants in mango and cashew orchards, respectively. In the case where thrips damage increased, overall crop yield increased by as much as 150% under ant treatments compared to the control (Anato et al., 2015), suggesting that increases in pest damage by thrips was still outweighed by overall benefits from *Oecophylla* spp. being present.

DISCUSSION

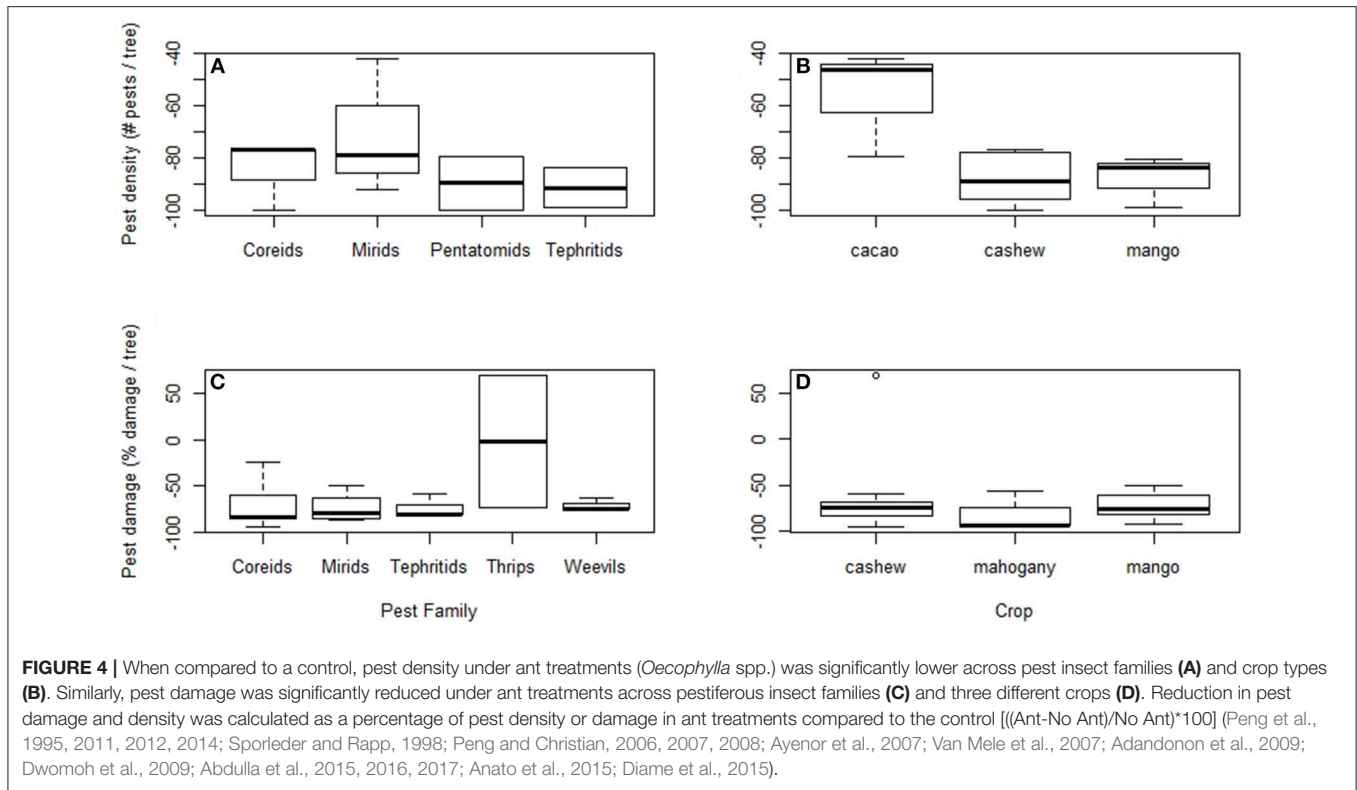
Weaver ants, like many other generalist arthropod predators, fill complex ecological roles in agroecosystems (e.g., Peng et al., 1999, 2014; Van Mele and Cuc, 2000; Peng and Christian, 2004; Pierre and Idris, 2013; Abdulla et al., 2015, 2017; Anato et al., 2017; Forbes and Northfield, 2017a). The ants have the potential to contribute beneficial ecosystem services by feeding on pest insects, but also could provide disservices when they shelter other herbivores with which they form trophobiotic relationships (Offenberg et al., 2013; Forbes and Northfield, 2017a), and/or when the ants prey upon beneficial arthropod predators and pollinators (Gonzalvez et al., 2013; Rodriguez-Girones et al., 2013; Figures 5A,C). Thus, it was perhaps surprising that our quantitative review for studies across studies from Africa, Australia, and Southeast Asia, from a diversity of pest complexes, and a range of tree crop species (Supplementary Table 1) yielded such consistently beneficial effects of *Oecophylla* ants (Figures 1–4). These benefits were robust across several pest families and species, the species of tree upon which ants were experimentally manipulated, and which of the two key *Oecophylla* species was being considered (Figures 1–4; Supplementary Figure 1). Thus, any concerns about weaver ants sufficiently degrading biological control or pollination to harm crop yields (e.g., Tsuji et al., 2004; Offenberg et al., 2013) appear to be largely rare and unwarranted. Indeed, it appears that any harm weaver ants cause to crops from harvesting homopterans, or deterring predators, parasitoids, and pollinators is outweighed by their benefits in pest reduction and increased yields (Figure 5B). Several lines of evidence suggest



that suppression of pests by ants can be as effective as insecticide applications for controlling pests (Figure 5B) (e.g., Peng and Christian, 2005b, 2007, 2008; Dwomoh et al., 2009; Abdulla et al., 2016, 2017), although ants might be most usefully deployed as one aspect of integrated pest management schemes that incorporate a range of tactics (Peng and Christian, 2005a).

The sole exception to the broader trend of *Oecophylla* spp. increasing crop yields was found when no profits were gained for a Thai mango orchard after a leafhopper pest, *Idioscopus clypealis* (Cicadellidae), wiped out the crop (Offenberg et al., 2013). In this study, the weaver ant *O. smaragdina* was observed protecting and harvesting honeydew from the leafhopper, in effect facilitating the pest's destruction of mango flowers (Offenberg et al., 2013). Additionally, a single study recorded an >150% increase in mealybug (Pseudococcidae) density in an Australian cacao orchard when weaver ants were

present (Forbes and Northfield, 2017a). In this case, mealybugs were not considered major cacao pests and their outbreak with ants present was not considered an ecosystem disservice (Forbes and Northfield, 2017a); however, crop yields were not measured and ant-mediated disservices cannot be entirely excluded in this case study. While our quantitative review revealed general benefits for crop yields despite concomitant benefits to some herbivores that the ants tend for honeydew, some caveats are needed. Some honeydew producers can be vectors for plant viruses or other pathogens (e.g., Parrella et al., 2003; Dzahini-Obiatey et al., 2006; Tsai et al., 2010), with the potential to yield infections that harm plants. Because weaver ants tend a wide diversity of potential pathogen vectors this indirect facilitation of plant diseases could be widespread if overlooked; for example, a survey of *O. smaragdina* in tropical northern Australia revealed that ants were engaged in trophobiotic relationships

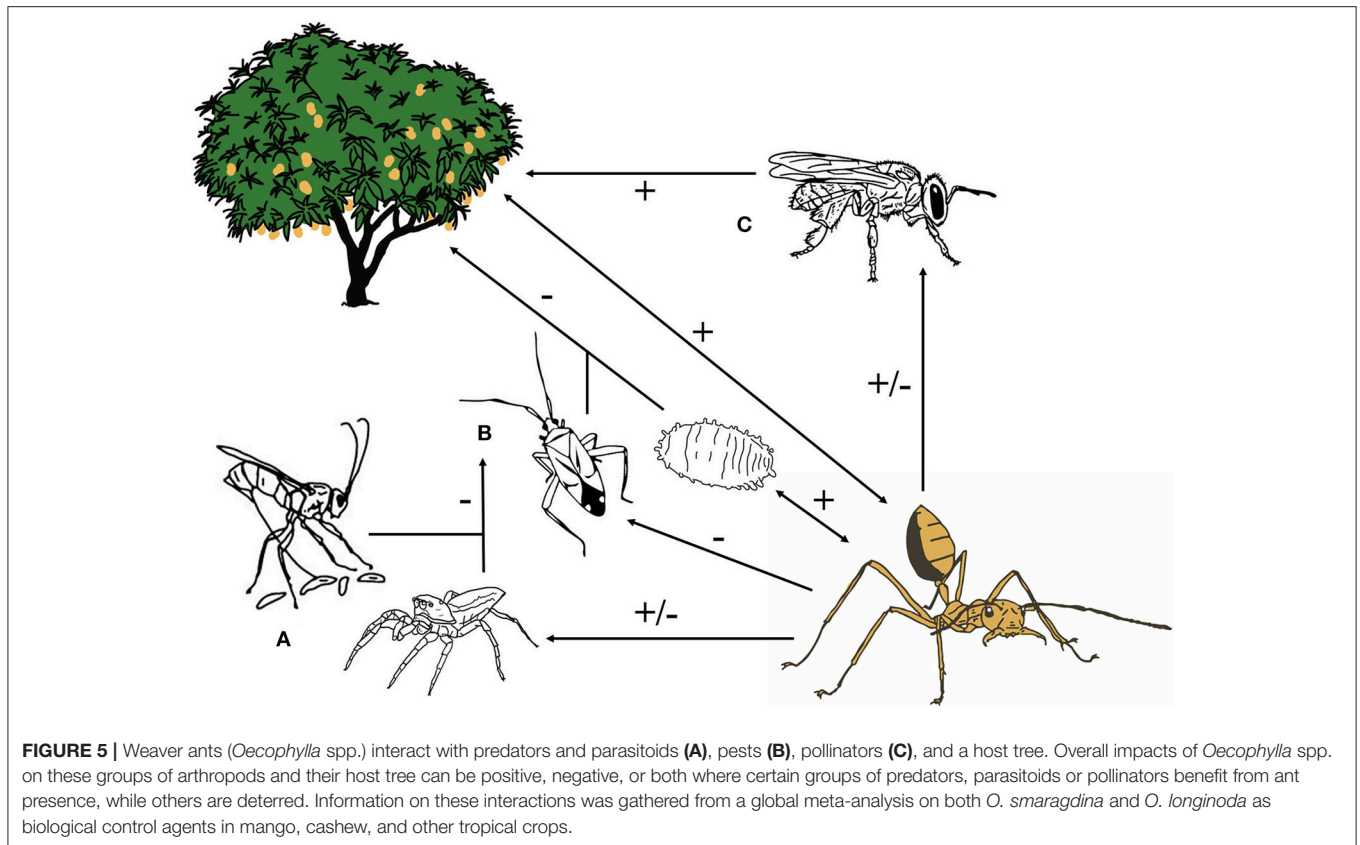


not only with homopterans such as scale insects (Coccidae, Psuedococcidae, and Margarodidae) and aphids (Aphidae), but also treehoppers (Membracidae), leafhoppers (Cicadellidae), and caterpillars (Lepidoptera: Lycaenidae) (Bluthgen and Fiedler, 2002). Surveys of potential honeydew producers and the diseases they may vector must therefore be closely monitored in weaver ant biocontrol programs.

The literature also includes many instances of weaver ants feeding on predatory insects (e.g., Vayssieres et al., 2015), including deterring predatory mantids (Ramesh et al., 2016), other beneficial ants (Philpott and Armbrrecht, 2006), and parasitoid wasps (Mathews et al., 2011; Appiah et al., 2014; Figure 5A). Weaver ants have also been observed deterring and capturing several pollinator species (Tsuji et al., 2004; Gonzalez et al., 2013; Rodriguez-Girones et al., 2013; Figure 5C). Thus it is perhaps surprising that net ant impacts were overwhelmingly positive for crop yields (Figure 3), rather than ants disrupting biological control through intense intraguild predation (e.g., Snyder and Ives, 2001) or weakening fruit set by deterring pollinators (Tsuji et al., 2004; see also, Huey and Nieh, 2017). Unfortunately, our literature search yielded only a few cases where other predators or pollinators (e.g., Vayssieres et al., 2015) were counted following weaver ant exclusion, preventing us from making a meaningful quantitative analysis of how the ants interact with other arthropod groups. Nonetheless, a careful reading of the literature presents several possible resolutions to this apparent conundrum. First, beneficial insects may represent a relatively small proportion of all prey taken by the ants. For example, in a mango orchard only five of

241 prey species captured by *O. longinoda* were predators or pollinators (Vayssieres et al., 2015). Second, weaver ants often co-exist with a suite of predators adapted to forage among ants such as the ant-mimicking mantis *Euantissa pulchra* (Ramesh et al., 2016), jumping spider ant-mimics such as *Cosmophasis bitaeniata* (Allan and Elgar, 2001), *Myrmarachne* sp. (Ceccarelli, 2009) and *Phintella piatensis* (Nelson and Jackson, 2009) and a suite of web-spinning spiders that co-exist with the ants (Forbes and Northfield, 2017b; Figure 5A). A similar situation has been reported for ant-pollinator interactions, where weaver ants were observed capturing and deterring stingless bees (*Nomia* sp.) on the shrub *Melastoma malabathricum* but not larger carpenter bees (*Xylocopa* sp.); because the carpenter bees were the most effective pollinators ants yielded no overall change in pollination efficiency (Gonzalez et al., 2013; Figure 5C). Altogether then, the apparent potential for widespread negative interactions between ants and beneficial insects may rarely be realized in real world agroecosystems. A few instances have been recorded, however, as parasitism rates of the mealybug *Rastrococcus iceryoides* (Pseudococcidae) decreased 35% (from 86.6 to 51.4%) in the presence vs. absence of tending weaver ants (Tanga et al., 2016). So, it remains possible that there are some cases of severe interference between weaver ants and beneficial insects that remain to be recognized.

While *Oecophylla* spp. has been observed feeding on floral and extra floral nectaries on their host trees (Rickson and Rickson, 1998; Bluthgen and Fiedler, 2002), along with other plant materials like seeds (Vayssieres et al., 2015), plant resources



have never been experimentally manipulated to measure impacts on weaver ant densities and impacts. Nutrient flow from the ants back to their host plant was inferred when Asian weaver ants (*O. smaragdina*) were fed ^{15}N -labeled glycine and the ant's fecal droplets were absorbed on coffee leaves (*Coffea arabica*). This in turn led to increased levels of total nitrogen and ^{15}N compared on leaves with than without ants (Pinkalski et al., 2018; see also Pinkalski et al., 2016; Vidkjaer et al., 2016). These direct nutrient exchanges from ants to their host plant are suspected to play a role in improving plant health (Pinkalski et al., 2018). This foliar uptake of ant-provided nutrients has only recently been recorded, but sheds light on the extent of possible mechanisms for nutrient exchange which may support a mutualistic relationship between *Oecophylla* spp. and a broad range of host trees. In general, there is a need for more work specifically documenting benefits of plant feeding for weaver ants, and vice versa.

In general, ants are abundant, cooperative and polyphagous, two characteristics which emphasize their potential to control pests in agroecosystems around the world (Philpott and Armbrrecht, 2006). Red imported fire ants (*Solenopsis invicta*) were previously recorded to have variable effects on arthropod communities in agroecosystems. However, a study on the relationship between fire ants and the cotton aphid (*Aphis gossypii*) explained some of this variation as the ants were more likely to forage and deter pests from cotton plants

with aphids (Kaplan and Eubanks, 2005). In effect, this ant-homopteran trophobiotic relationship facilitated ant impact on the cotton arthropod community where roughly 27% of herbivore and 54% of predator taxa were adversely effected (Kaplan and Eubanks, 2005). Similarly, *Azteca* ants harvest scale insects and the ants' presence in coffee plantations has a negative relationship with potential herbivores (Vandermeer et al., 2002). These trophobiotic relationships between ants and honeydew-producing insects may facilitate biological pest suppression (Styrsky and Eubanks, 2007). In a review of ants harvesting trophobionts, this relationship was found to indirectly benefit host plants in the majority of cases as the density of more antagonistic herbivores were reduced (Styrsky and Eubanks, 2007). Interference in pollination from ant-guards also seems relatively rare as plants and their ant guards have evolved different mechanisms to promote plant-ant health. For instance, ant-guards (such as *Crematogaster* spp.) on *Acacia* trees are deterred from early flower dehiscence to allow pollinator access (Willmer and Stone, 1997). Additionally, ant guards (*Crematogaster* spp.) of the myrmecophytic plant *Macaranga winkleri* are prevented from interfering with pollination as the primary pollinators, thrips (*Dolichothrips fialae*), produce an ant-repelling acid from their anuses (Yamasaki et al., 2016). Overall, we see ant-plant (Yamasaki et al., 2016) and ant-trophobiont (Kaplan and Eubanks, 2005) nutrient exchanges facilitating ant-defense of

plants with novel strategies to avoid conflicts of interest like decreased pollination.

Previous reviews of generalist predators have found that generalists can significantly reduce pest species in agroecosystems (Symondson et al., 2002; Offenberg, 2015). Symondson et al. (2002) found that approximately 75% of case studies showed that pest species were significantly reduced under generalist predator treatments. In order to be successful in biological control programs, generalist predators must maintain a high population density when pest populations decline, be opportunistic in feeding habits in order to maintain that population abundance, and exploit attacks by resurgent pests (Symondson et al., 2002). These characteristics can be found in generalist predators which supplement their diet by feeding on their host plant (Eubanks and Denno, 1999). Big-eyed bugs, *Geocoris punctipes* (Geocoridae) are omnivorous predators which supplement their predatory diet by feeding on lima bean pods (Eubanks and Denno, 1999). When prey density is low or of poor quality, these predators can be sustained based on the quality of their host plant (Eubanks and Denno, 1999). Overall, host-plant feeding, appears to sustain generalist predators through prey scarcity and improve biological pest suppression.

Ecosystem services are the products of complex interactions and we emphasize the importance of crop, pest, pollinator, and predator context for when these services may be reaped. We also suggest that host-plant feeding, whether directly or indirectly through trophobionts, may be a predictive variable for when generalist predators provide ecosystem services. The classification of host-plant feeding as an ecosystem disservice is also largely context specific as no instances of direct crop damage from generalist predators was found in this review and indirect damage cause by predators via their trophobionts primarily occurs when certain diseases are present (Forbes and Northfield, 2017a). Weaver ants (*Oecophylla* spp.) have been shown to effectively reduce pest damage and density from a suite of arthropods and increase crop yields around the world.

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The case-dependency of when their trophobiotic relationships become antagonistic, however, must be further investigated. Further research on the dynamics of nutrient exchanges between ants, trophobionts, and plants, particularly when this nutrient exchange may be critical to pest suppression, remains to be investigated. Additionally, the interactions that *Oecophylla* spp. have with other beneficial arthropod taxa should be explored for agroecosystems to record the impact of ants on pollination, predation, and parasitism. These insights may then shed light on the context-dependent cases for when ecosystem services from ants and other plant-feeding generalist predators may be most reliably achieved.

AUTHOR CONTRIBUTIONS

JT developed the paper, conducted the quantitative literature review, wrote and revised the body of the text, performed statistical analyses, and created all figures in R and original illustrations using Photoshop. TN helped develop the paper, revised drafts of the manuscript, conducted statistical analyses, and assisted in creating figures in R. WS helped develop the paper and revised drafts of figures and the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2019.00120/full#supplementary-material>

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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