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Oecophylla smaragdina ants provide pest control in Australian cacao.

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ABSTRACT

Ecosystem service-driven methods of agricultural production that make optimal use of an ecosystem's natural services are often effective in smallholder crops, leading increases in habitat heterogeneity at large spatial scales that encourage beneficial species. Pollination services in cacao farms can be enhanced through efforts to conserve pollinator habitats, such as adding cacao fruit husks underneath trees to provide habitat and food resources for midge pollinators. However, it remains unclear how this habitat manipulation affects pest densities or biological control. Here, we evaluated the effects of the predaceous ant *Oecophylla smaragdina* on three major pests of Australian cacao (*Helopeltis* spp., *Amblypelta* spp. and *Rhyparida nitida*) in an Australian cacao farm, in the presence and absence of cacao fruit husks. We also evaluated the effect of *O. smaragdina* on their potentially plant-damaging, mutualistic mealybug (Pseudococcidae) partners in the presence and absence of cacao fruit husks. *O. smaragdina* reduced the combined densities of *Helopeltis* spp. and *Amblypelta* spp., regardless of cacao fruit husk addition. The ants also reduced the densities of *R. nitida* in the absence of cacao fruit husks, but *R. nitida* densities were naturally low in the experimental plots that received the addition of cacao fruit husks, regardless of ant presence. In contrast, ants generally increased the densities of mealybugs. These data suggest that *O. smaragdina* ants provide pest control services for three major insect pests in Australian cacao farms. Furthermore, this control may be compatible with habitat manipulations (*i.e.*, the addition of cacao fruit husks) to improve pollinator habitat.

Key words: Amblypelta; agriculture; biological control; cocoa, Helopeltis; mealybugs; mutualism; wet tropics.

CACAO (*THEOBROMA CACAO* L., MALVACEAE) IS A TROPICAL UNDERSTORY TREE NATIVE TO THE NORTHERN PARTS OF SOUTH AMERICA, from which the global commodity cocoa is produced (Motamayor *et al.* 2002, Omolaja *et al.* 2009). Although a major global commodity, cacao is largely cultivated by smallhold farmers on individual, family-managed farmlands typically ranging 0.5 to 7 ha in size (Clay 2004) in the lowland tropical regions of Latin America, West Africa and Indonesia (Franzen & Mulder 2007). The increasing global demand for cocoa has consequently led a worldwide push towards the intensification of cacao cultivation for increased productivity (Schroth & Harvey 2007), moving cacao production further from the traditionally managed, sustainable cacao cultivation systems of the past (Somarriba *et al.* 2004, Somarriba *et al.* 2014) .

Ecologically driven management strategies of cacao production that make optimal use of an ecosystem's natural services (*e.g.*, pest control by natural enemies of pests) rather than relying upon artificial inputs (*e.g.*, pesticide application to control pests) to manage cacao, may benefit tropical smallholder agricultural systems (Perfecto *et al.* 2007, Perfecto & Vandermeer 2010, Clough *et al.* 2011), where intensified agricultural models typified by high chemical input dependence are economically unsustainable (Tittonell & Giller 2013). Further, ecologically driven management strategies of agricultural production can potentially reduce the environmental externalities of intensified agriculture (*e.g.*, lethal effects of pesticide application on non-target beneficial insects) and lead increases in both agricultural production (Bommarco *et al.* 2011) and biodiversity (Reitsma *et al.* 2001). Nonetheless, cacao cultivation is transitioning from traditional, less intensive agroforestry cultivation systems (*i.e.*, limited agrochemical use, limited mechanisation and where cacao is grown together with a diversity of other tree and crop species (Somarriba *et al.* 2001)) that support higher levels of biodiversity (Reitsma *et al.* 2001), to modernized and intensified monoculture cacao production models (Gockowski & Sonwa 2011). For example, in Australia where cacao has only recently been cultivated for commercial production, cacao farms predominantly comprise high-density monoculture farms with trees organized in linear rows, intensively managed using mechanized management tools (*e.g.*, tractor, lawn-mower) and artificial agrochemical inputs (*e.g.*, fertilizer, pesticide and herbicide) (Diczbalis *et al.* 2010). Internationally, the transition to intensified cacao systems has included an increased reliance upon chemical pest management (Perfecto & Castiñeiras 1998), possibly in response to predator declines and increased pest outbreaks linked to agricultural intensification (Klein *et al.* 2002). This increased use of chemical pest control may contribute to the pollination deficits recently observed in cacao crops (Brittain *et al.* 2010, Groeneveld *et al.* 2010, Bommarco *et al.* 2013). Therefore, the identification of biological alternatives to chemical pest control, including identifying natural enemies of pests, is an important step in improving the provision of pollination services and crucial for ecologically and economically sustainable cacao production. Furthermore, similarities between the responses of some predators and pollinators to habitat management practices (Bianchi *et al.* 2006) suggest that the potential for biological control agents in cacao should be evaluated in the context of strategies used to encourage other ecosystem services such as pollination, as part of a more holistic approach to farming. In cacao, one such strategy used to encourage pollinators is to apply decomposing cacao fruit husks as mulch to reduce the effects of habitat simplification on cacao pollinators (Adjaloo *et al.* 2013). The effectiveness of this habitat manipulation may be attributable to the increased availability of alternative habitat and food resources for pollinators, however the effects of this habitat manipulation on predators and their role in the biological control of pests are yet to be determined. Thus, the effectiveness of biological control by natural enemies of pests should be considered in the presence of cacao fruit husk addition.

Ants provide important biological services in tropical agroecosystems (Perfecto & Castiñeiras 1998), including pest control by predatory ants (Way & Khoo 1992). However, the pervasive mutualistic association of some ants with hemipterans can overshadow the benefits they provide to crop production (Way 1963). Therefore, the relative impacts of ants on particular herbivorous pests are important to consider when describing the ecological role of ants in agroecosystems. For example, *Dolichoderus thoracicus* ants are known to successfully control multiple insect pests of cacao in Malaysia and Indonesia, where their successful deterrence of major cacao pests such as heteropteran mirids (Hemiptera: Miridae) and the lepidopteran cocoa pod borer *Conomorpha cramerella* (Snellen) seems to outweigh their potentially negative association with a number of hemipteran mealybug (Pseudococcidae) species (Khoo & Chung 1989, Way & Khoo 1991, See & Khoo 1996). This is in large part due to the low economic impact from mealybugs relative to other pests in these regions (Perfecto & Castiñeiras 1998).

Oecophylla smaragdina ants are commonly found in the cacao farms of northern Australia and have long been recognised as beneficial predators of pests in tropical cropping systems (Way & Khoo 1992, Van Mele 2008). This marked control of pests in other crops suggests great potential for *O. smaragdina* in Australian cacao systems as well. In Australian cacao farms, the major insect pests damaging cacao trees are the mirids (*Helopeltis* spp.), fruit-spotting bugs (*Amblypelta* spp.) (Hemiptera: Coreidae) and black swarming leaf beetles (*Rhyparida nitida* Clark)

(Coleoptera: Chrysomelidae) (Diczbalis *et al.* 2010). Although research demonstrating reduced cacao yields from these herbivorous insect pests has not been conducted in Australian cacao farms, it is generally accepted amongst farmers and state government agricultural services that these pests can cause economically significant damage to both young cacao fruits and *T. cacao* seedlings (Diczbalis *et al.* 2010). Also found in Australian cacao farms are mealybugs. In other cacao growing regions such as West Africa, mealybugs play a major role in the transmission cocoa swollen shoot virus (Dzahini-Oblatey *et al.* 2006), a severely damaging badnavirus causing defoliation, dieback, yield losses and tree mortality in cacao (Muller & Sackey 2005). However, as cocoa swollen shoot virus is not currently present within Australian cacao farms, disease transmission by mealybugs is not a major concern and damage caused by mealybugs is likely minimal.

Effective natural predators of the three major insect pests present within Australian cacao systems are yet to be identified and an efficient biological control program, as an alternative to chemical pest management, is unavailable to facilitate the adoption of ecologically sustainable cacao farm management practices within Australia. Given the biological control efficiency of *O. smaragdina* in other tropical crops (Way & Khoo 1992, Van Mele 2008), we conducted a field manipulation study to investigate the effectiveness of *O. smaragdina* in the control of three major insect pests (*Helopeltis* spp., *Amblypelta* spp. and *Rhyparida nitida*) on a commercially active Australian cacao farm. Further, as *O. smaragdina* ants often involve mutualistic associations with herbivorous mealybugs that vector disease in other cacao production systems (Muller & Sackey 2005) and can cause significant negative impacts on plant health in other crop systems (Styrsky & Eubanks 2007), we also investigated the effect of *O. smaragdina* on mealybug density. Finally, we evaluated the effectiveness of pest control services by *O. smaragdina* on each herbivore species in the presence of a recently developed method to improve pollination rates, the addition of cacao fruit husks underneath cacao trees (Adjaloo *et al.* 2013) to determine whether management strategies used to promote biological pest control services provided by *O. smaragdina* ants are compatible with agricultural practices employed to support pollinators and pollination services.

METHODS

STUDY SITE.− The study site, Whyanbeel Valley Cocoa Estate (145°21'E, 16°22'S) includes a conventional monoculture farm where trees are organized in linear tree rows. The planting material includes three self-compatible Trinitario SG2 hybrid *T. cacao* varieties developed at the Papua New Guinea Cocoa and Coconut Research Institute. Within the farm, we established fourteen randomized experimental plots, with each plot containing a total of eight trees organized as two parallel rows of four trees per row (Figure 1A).

EXPERIMENTAL DESIGN.−To examine the effects of *O. smaragdina* on the densities of herbivorous insects (*Helopeltis* spp., *Amblypelta* spp., *R. nitida* and mealybugs) on cacao trees, within each experimental plot two differing *O. smaragdina* ant treatments were randomly assigned and replicated twice within each plot row (Figure 1B, C). The two differing ant treatments included an 'ant presence' (ants) treatment, in which *O. smaragdina* ants were allowed to forage on trees and an 'ant exclusion' (no ants) treatment where *O. smaragdina* ants were excluded from trees. *O. smaragdina* ants were excluded from trees assigned the ant exclusion treatment by physically removing the nests of any present ant colonies and by applying ant barriers around the trunks of the trees, preventing ant movements along the trunk. Ant barriers involved a base layer of thick cotton batting (height: 15 cm; width: 2 cm) to protect the trunk and a layer of black duct tape (50 mm) on top of the batting material. The duct tape was sealed over itself to secure the ant barrier around the trunk tight enough to exclude *O. smaragdina* ants from movement underneath the ant barrier. For trees assigned the ant exclusion treatment, a thick layer of Tangle-Trap (Tanglefoot, Contech, Victoria, Canada) was applied on top of the duct tape to completely encircle the tree trunk and inhibit ant movements onto the tree. We pruned the canopy foliage on all experimental trees to disrupt canopy connectivity and inhibit the movements of ants between canopies of neighbouring trees. Pruning of canopy foliage in this manner was continued throughout the duration of the experiment to maintain canopy dis-connectivity. The ant presence treatments were identical to the ant exclusion treatments in experimental design, but did not receive the Tangle-Trap application, allowing *O. smaragdina* ants to move up and down the tree trunk over the ant barriers. For each ant presence tree where *O. smaragdina* were not observed, we transplanted an active *O. smaragdina* nest to the tree (*as in* Peng & Christian (2005b)). Ant barriers were applied to trees on 17 November 2014 and the Tangle-Trap required for the ant exclusion treatments was applied on 19 November 2014 after the removal of present ant colonies and canopy foliage pruning.

To evaluate effects of cacao fruit husk addition on biological control by *O. smaragdina*, all ant treatments were nested within plots selected for one of two cacao fruit husk treatments (Figure 1B, C). Seven of the fourteen plots were randomly selected for a ‘with cacao husk’ treatment, in which approximately 280 kg (35 kg per tree) of fresh cacao fruit husks left over from processing were placed underneath all trees within the selected plots. The remaining seven plots were assigned the 'no cacao husk' treatment, where they did not receive the addition of cacao fruit husks. The 'with cacao husk' treated plots were spaced at a minimum of 15 m away from the 'no cacao husk' treated plots to reduce the possibility of treatment effect spillover between the two cacao husk treatments (Figure 1A). The two *O. smaragdina* treatments (ants: n = 28 trees; no ants: n = 28 trees) were nested equally within the two cacao fruit husk treatments (with cacao husk: n = 56 trees; no cacao husk: n = 56 trees). Using a split-plot design, two trees per plot row were randomly assigned to one of the two ant treatments, regardless of cacao husk treatment. Thus, a total of 28 replicate trees for each of the two ant treatment types were present within each of the two cacao husk treatments.

O. SMARAGDINA AND INSECT SURVEYS.−Field surveys measuring the density of each insect species were conducted fortnightly from December 2014 to March 2015, during the morning hours between 0700 h and 1200 h. On each observation date, we visually surveyed each tree within each experimental plot for a period of 3 minutes. During the observation period, the entirety of all trees (foliage, branches, trunk) was actively surveyed, recording all observed *O. smaragdina* ants, mirids (*Helopeltis* spp.), fruit-spotting bugs (*Amblypelta* spp.), leaf swarming beetles (*R. nitida*) and mealybugs. All insects were identified to family and where possible, species. To reduce the effects of daily weather fluctuations on the fortnightly surveys, under conditions of heavy rainfall or high wind, monitoring was postponed to the next appropriate day.

STATISTICAL ANALYSIS.−We used generalized linear mixed models in proc mixed using SAS ® software version 9.04 (SAS 2015) to evaluate the effects of ant exclusion (ant presence versus ant exclusion), cacao fruit husk addition (cacao husk addition versus no cacao husk addition) and sample date, as well as all potential interactions on the density of each insect group surveyed. Each generalized linear mixed model included a random effect of plot and an autoregressive heterogeneous covariate structure to describe covariance between sample dates for the same tree. We grouped all mealybug species together due to difficulties identifying species in the field. We also grouped *Helopeltis* spp. and *Amblypelta* spp. together, due to their similar biology (similar size, phloem feeding nature, broader taxonomic grouping and response to ants in other studies (Peng *et al.* 1997, Peng *et al.* 2012, Wielgoss *et al.* 2014)) and low densities. For the statistical analysis of *R. nitida* beetle density, we only included beetle counts from the four sample dates between 20 January and 5 March, due to low densities on the first three sample dates.

For each response variable (*O. smaragdina*, heteropterans, *R. nitida* and mealybugs), we used AIC scores to evaluate multiple assumptions of distributions and covariance structures and selected the most appropriate option. We assumed the densities of each *O. smaragdina* ants, *R. nitida* beetles and mealybugs followed a negative binomial distribution. We modeled temporal autocorrelation in *O. smaragdina* ant densities with a general Toeplitz covariance structure and added further detail by using an autoregressive structure for mealybugs and an autoregressive heterogeneous structure for *R. nitida* beetles. Due to numerous zero-counts in the analysis of heteropteran densities, the negative binomial distribution fit these data poorly. Thus, we used two approaches to analyze these data. First, we analyzed $\log_{10}(x + 1)$ transformed insect counts with a Gaussian distribution and autoregressive heterogeneous covariance structure. We then modeled the presence of heteropterans with a binomial distribution. Due to the reduced power inherent in analyzing presence/absence data, we used a simplified model only evaluating the main effects of *O. smaragdina* presence, cacao fruit husk presence and time, using a compound symmetry covariance structure to describe the covariance for a given tree.

RESULTS

O. SMARAGDINA. —The ant exclusion treatment was successful at reducing ant densities, with the number of *O. smaragdina* ants per tree significantly greater in trees selected for the ant presence treatment ($F_{1,\,743} = 41.49$, $P < 0.0001$; Fig. 2A, B) than trees selected for the ant exclusion treatment. The cacao fruit husk treatments had no direct influence on *O. smaragdina* density (cacao fruit husk treatment effect: $F_{1,\,743} = 0.02$, $P = 0.8939$; Fig. 2A, B), or on the effectiveness of ant treatments (cacao fruit husk treatment × ant treatment interaction: $F_{1,\,743} = 0.05$, $P = 0.8237$). *O. smaragdina* density significantly varied over time ($F_{6,\,743} = 2.37$, $P = 0.0281$; Fig. 2A, B) and ant density was dependent upon the cacao fruit husk treatment ($F_{6,\,743} = 3.30$, $P = 0.0033$), with ant exclusions less effective on the first and final sample dates in the with cacao husk treated plots (Fig. 2B). This also appeared to drive a significant interaction between ant treatment, cacao fruit husk treatment and time on *O. smaragdina* densities ($F_{6,\,743} = 5.04$, $P < 0.0001$; Fig. 2). There was no significant interaction between time and ant treatment on *O. smaragdina* densities ($F_{6,\,743} = 1.83$, $P = 0.0899$).

HETEROPTERAN INSECTS (HELOPELTIS SPP. & AMBLYPELTA SPP.). —Heteropteran insect densities were significantly lower in trees selected for the ant presence treatment than in trees selected for the ant exclusion treatment ($F_{1,\,742} = 4.44$, $P =$

0.0354; Fig. 3A, B). The cacao fruit husk treatment had no direct effect on heteropteran insect density (cacao fruit husk treatment effect: $F_{1,\,742} = 0.31$, $P = 0.5769$; Fig. 3A, B) and did not influence the effect of *O. smaragdina* ants on heteropteran insect density (cacao fruit husk treatment × ant treatment interaction: $F_{1,\,742} = 0.03$, $P = 0.8624$; Fig. 3A, B). There was significant variation in heteropteran density over time ($F_{6,\,742} = 6.07$, $P < 0.0001$; Fig. 3A, B), but no significant interaction was found between time and either ant treatment ($F_{6,\,742} = 1.02$, $P = 0.4100$; Fig. 3A, B) or cacao fruit husk treatment ($F_{6,\,742} = 0.79$, $P = 0.5776$; Fig. 3A, B). There was no significant three-way interaction between ant treatment, cacao fruit husk treatment and time on heteropteran insect densities ($F_{6,\,742} = 0.51$, $P = 0.8036$). Heteropterans were more likely to be present in trees assigned the ant exclusion treatment ($F_{1,\,761} = 9.48$, $P = 0.0022$; Fig. 3A, B). The presence of heteropterans was variable through time ($F_{6,\,761} = 8.62$, $P < 0.0001$; Fig. 3A, B) though heteropteran presence showed no temporal variation in plots assigned the cacao fruit husk treatment ($F_{1,\,761} = 0.08$, $P = 0.7713$; Fig. 3B).

RHYPARIDA NITIDA. —The densities of *R. nitida* leaf beetles, when beetles were common in our plots (weeks 20 January through 5 March) were significantly lower in trees selected for the ant presence treatment, than in trees selected for the ant exclusion treatment ($F_{1,\,419} = 21.48$, $P < 0.0001$; Fig. 3C, D). However, the effect of ant treatment on *R. nitida* density was significantly greater in plots selected for the ‘no cacao husk’ treatment, than those plots selected for the ‘with cacao husk’ treatment (cacao fruit husk treatment × ant treatment interaction: $F_{1,\,419} = 8.23$, $P = 0.0043$; Fig. 3C, D). There was no direct influence of cacao fruit husk treatments on *R. nitida* density (cacao fruit husk treatment effect: $F_{1,\,419} = 0.38$, $P = 0.5393$; Fig. 3C, D).

Across dates from 20 January 2015 through 5 March 2015 there was no temporal variation in *R. nitida* density ($F_{3, 419} = 3.30$, $P = 0.0205$; Fig. 3C, D), or any interaction effect between time and either ant treatment ($F_{3, 419} = 1.85$, $P = 0.1369$; Fig. 3C, D) or cacao fruit husk treatment ($F_{3, 419} = 0.11$, $P = 0.9549$; Fig. 3C, D). There was also no significant three-way interaction between ant treatment, cacao fruit husk treatment and time on *R. nitida* densities ($F_{3, 419} = 1.42$, $P = 0.2371$).

MEALYBUGS. —Mealybug densities were significantly greater in trees selected for the ant presence treatment, than in the trees selected for the ant exclusion treatment ($F_{1, 743} = 10.00$ $P < 0.0016$; Fig. 2C, D). The cacao fruit husk treatments had no direct influence on mealybug density (cacao fruit husk treatment effect: $F_{1, 743} = 0.79$, $P = 0.3736$; Fig. 2C, D), or on *O. smaragdina*-mediated effects on mealybug density (cacao fruit husk treatment × ant treatment interaction: $F_{1, 743} = 0.15$, $P = 0.6954$; Fig. 2C, D). There was no significant variation in mealybug densities over time ($F_{6, 743} = 2.27$, $P = 0.0351$; Fig. 2C, D) and no significant interaction between time and either ant treatment ($F_{6, 743} = 1.61$, $P = 0.1422$; Fig. 2C, D) or cacao fruit husk treatment ($F_{6, 743} = 0.68$, $P = 0.6691$; Fig. 2C, D). There was also no significant three-way interaction between ant treatment, cacao fruit husk treatment and time on mealybug densities ($F_{6, 743} = 1.99$, $P = 0.0650$).

DISCUSSION

We found that *Oecophylla smaragdina* ants reduced the densities of two major insect pests of cacao in Australia: the mirids and the fruit-spotting bugs (*Helopeltis* spp. and *Amblypelta* spp. respectively) and the addition of cacao fruit husks as a mulch did not disrupt the ability of *O. smaragdina* to reduce the densities of these pests. Our results support similar findings in other Australian tropical fruit crops (*i.e.*, cashew and mango), in which *O. smaragdina* were found an economically important biological control agent for both mirids (*Helopeltis pernicalis* Stonedahl *et al.* and fruit-spotting bugs (*Amblypelta lutescens* Distant) (Peng *et al.* 1995, Peng *et al.* 1997, Peng & Christian 2005a, Peng & Christian 2005b). We also found *O. smaragdina* ants are effective in reducing the densities of *Rhyparida nitida* leaf beetles when cacao fruit husk mulch is absent, but may not be necessary when cacao fruit husks are applied as a mulch. This interaction appears due to low *R. nitida* beetle densities in the 'with cacao husk' treated plots even in the absence of ants, rather than attributable to poor control by *O. smaragdina*. The low *R. nitida* densities in the 'with cacao husk' treated plots may be due to the dispersal of *R. nitida* beetles outside of the plots, or due to within-plot mechanism (*e.g.*, unsuitable habitats for *R. nitida* reproduction and/or survival or increased predation on *R. nitida* beetles mediated by habitat-related increases in predator densities). In a concurrent study we found that in addition to increasing pollination rates, the addition of cacao fruit husks as mulch underneath trees, increased the densities of native spider and skink predators (Forbes 2015). Thus, it is possible that increased native predator densities within the 'with cacao husk' treated plots, helps to maintain low insect pest densities in the absence of the predaceous *O. smaragdina* ants.

Biological control by ants is achieved by directly preying upon pest insects, by chemically deterring pest insects and by causing pest insects to drop from the host plant to the ground when harassed by predatory ants (Way & Khoo 1992) where other predators might consume them (Philpott *et al*. 2004, Philpott & Armbrecht 2006). In the current study, *O. smaragdina* ants were regularly observed capturing and transporting all three major insect pests (*Amblypelta* spp., *Helopeltis* spp., and *R. nitida*) back to the nest, indicating that direct predation by *O. smaragdina* is likely a major mechanism driving the observed reductions in insect pest densities. However, *O. smaragdina* ants also produce a conspicuous, long-lasting recruitment odour trail that remains strong for at least 24 hours and persists for three days (Jander & Jander 1979). Insects can identify olfactory cues associated with predation (Abbott 2006, Gonçalves-Souza *et al.* 2008, Goodale & Nieh 2012), including *O. smaragdina* recruitment odour trails that may aid predator detection and avoidance by plant-visiting herbivorous insects (Li *et al.* 2014). For example, Offenberg *et al.* (2004) report that *R. wallacei* beetles can detect and actively avoid *O. smaragdina* pheromone. Thus, predator detection and avoidance may be an additional mechanism driving the reductions in pest densities in trees inhabited by *O. smaragdina* ants observed in our study.

Our results suggest that *O. smaragdina* may serve as an effective biological control agent for heteropteran and *R. nitida* pest insects in Australian cacao. However, *O. smaragdina* ants were found to increase the densities of hemipteran mealybugs. This observed increase is not surprising considering the proclivity of *O. smaragdina* to tend hemipterans and harvest their sugary honeydew exudate (Bluthgen & Fiedler 2002). In cacao, likely the most economically significant role of mealybugs is in the transmission of cocoa swollen shoot virus (Dzahini-Oblatey *et al.* 2006). Fortunately, cocoa swollen shoot virus is not present in Australia, so the potential for economic damage caused by the *O. smaragdina*-mediated increases in mealybug densities observed in our experiments is likely minimal. Nonetheless, further experimental work is required to determine the per-capita effects of each pest species on cacao yields and whether the benefits of pest suppression by *O. smaragdina* outweigh the negative impacts of *O. smaragdina* on cacao production through their tending and promotion of mealybugs.

Phloem-sucking hemipterans are commonly regarded as one of the most damaging groups of plant pests worldwide as they consume plant phloem, damage plant tissues and may vector toxins and disease in many plants of economic importance (Carver *et al.* 1991, Culik & Gullan 2005). However, while the presence of both ants and hemipterans may indirectly benefit the host plant whilst hemipteran densities remain low (Way 1963, Cushman & Addicott 1991, Styrsky & Eubanks 2007), at high densities hemipterans can reduce plant fecundity or increase plant mortality (Styrsky & Eubanks, 2007). This positive effect on hemipterans suggests the total benefits of ants in biological control may depend on the magnitude of their impact on the densities of the hemipterans they tend, relative to their role as predators of other pests (Way & Khoo 1992). Several studies have addressed the dual function of ants in agricultural systems as predators of pests and hemipteran tenders, with some demonstrating an overall net benefit of ants in agroecological systems. For example, in Mexican coffee farms, a diverse group of ants significantly reduce the major pest insect, coffee berry borer *Hypothenuemus hampei*, however they also tend the less damaging scale insects (Gonthier *et al.* 2013). Similarly, in Indonesian cocoa farms, *Dolichoderus* spp. ants reduce the densities of major pests including *Helopeltis* spp. true bugs and *Conopomorpha* spp. moths, thus reducing herbivory and indirectly increase fruit set, presumably by increasing plant nutrient availability (Wielgoss *et al.* 2014). The same study also found that ants increased mealybug densities and contributed to the spread of fungal pathogens, but that the positive effects outweighed the negative effects, with higher yields in the presence, rather than absence, of *Dolichoderus* spp. ants. In cases where high densities of ants' mutualistic partners can become damaging, the conservation of diverse predator communities may help to maintain relatively low hemipteran densities (*e.g.*, Francis *et al.* 2012). For example in Mexican coffee farms, ants provide biological control of coffee berry borers, while parasitic phorid flies and predaceous lady beetles reduce the densities of ants and the scale insects they tend, respectively (Vandermeer *et al.*, 2010). Taken in sum, ants can play a critical role in the provision of biological control ecosystem services in tropical agroecosystems.

Enhancement of ecosystem services in agriculture, often called ecological intensification, has drawn increasing attention to the ways in which organisms contribute to the delivery of ecosystem services (Kremen & Ostfeld 2005, Díaz *et al.* 2007, Luck *et al.* 2009). While the current demand for ecosystem services is growing rapidly (*e.g.*, Beier *et al.* 2008, Loring *et al.* 2008, Carpenter *et al.* 2009), uncertainty remains as to how to manage the provision of multiple ecosystem services simultaneously. In some cases, as may be the case in the improvement of pollination and biological control, identifying synergies between management strategies employed for individual ecosystem services may improve our ability to manage multiple, perhaps complimentary, ecosystem services (Lundin *et al.* 2012, Shackleford *et al.* 2013). Previous studies evaluating such synergies have ranged from documenting trade-offs such as predator conservation that disrupts pollination services (Knight *et al.* 2006), to synergistic management strategies such as natural (or semi-natural) habitat promotion (Diekotter *et al.* 2010) and integrated pest management systems (Dale & Polasky *et al.* 2007) that simultaneously promote pollinators, predators of pests and the ecosystem services they provide (Stallman 2011). Here, we found that habitat management to promote pollination ecosystem services in cacao agriculture did not disrupt biological pest control services. A greater mechanistic understanding of cases such as this may lead to improved management of multiple ecosystem services in other agroecosystems.

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FIGURE LEGENDS

FIGURE 1. Diagrammatic representations of (A) example experimental plot placement and spacing within the greater *T. cacao* plantation; (B) example experimental ant treatment design nested within plots assigned the ‘With cacao husk’ treatment; and (C) example experimental ant treatment design nested within plots assigned the ‘No cacao husk’ treatment. Individual experimental plots each comprise eight *T. cacao* trees, organized as two parallel rows of four consecutive trees. Within each plot, regardless of cacao husk treatment (With cacao husk; No cacao husk), two differing ant treatments (Ants; No ants) were randomly assigned and replicated twice within each plot row.

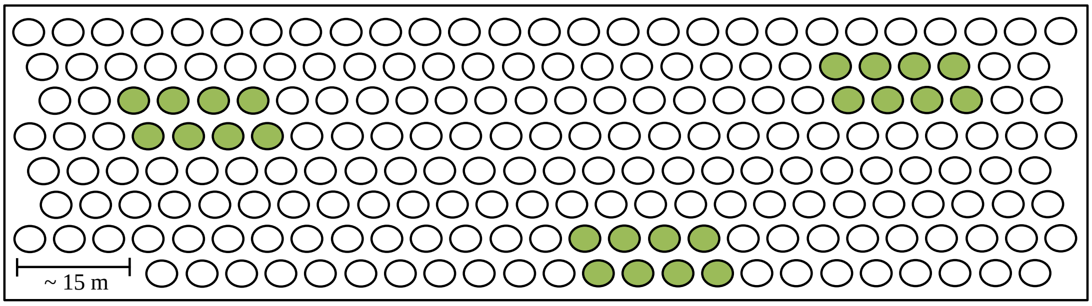
FIGURE 2. Mean (± SE) *O. smaragdina* (A, B) and mealybugs (C, D) density per tree surveyed from 11 December 2014 to 5 March 2015, when subject to ant presence (Ants) and exclusion (No ants) treatments, in plots without (A, C) and with (B, D) cacao fruit husks underneath trees.

FIGURE 3. Mean (± SE) heteropterans (*Helopeltis* spp. & *Amblypelta* spp.) (A, B) and *Rhyparida nitida* (C, D) density per tree surveyed from 11 December 2014 to 5 March 2015, when subject to ant presence (Ants) and exclusion (No ants) treatments, in plots without (A, C) and with (B, D) cacao fruit husks underneath trees.

FIGURES

FIGURE 1.

A) Example of plot placement within *T. cacao* plantation



B) Example treatment design in 'With cacao husk' plots

C) Example treatment design in 'No cacao husk' plots

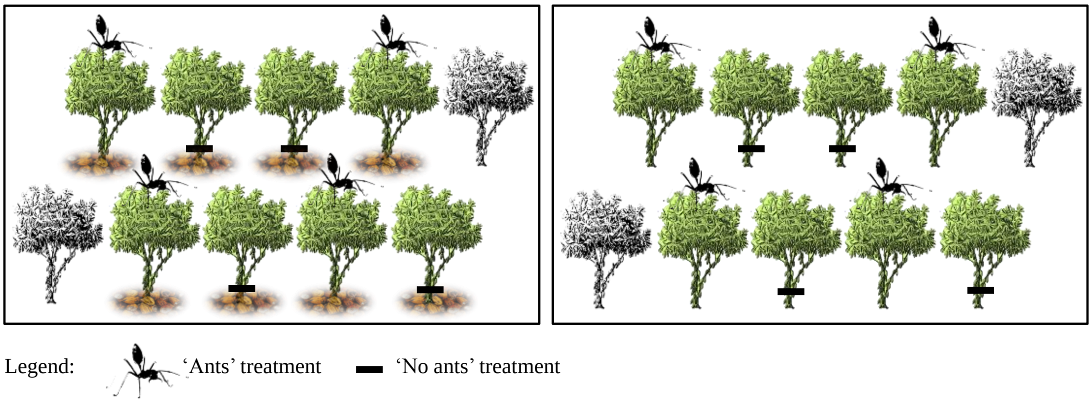


FIGURE 2.

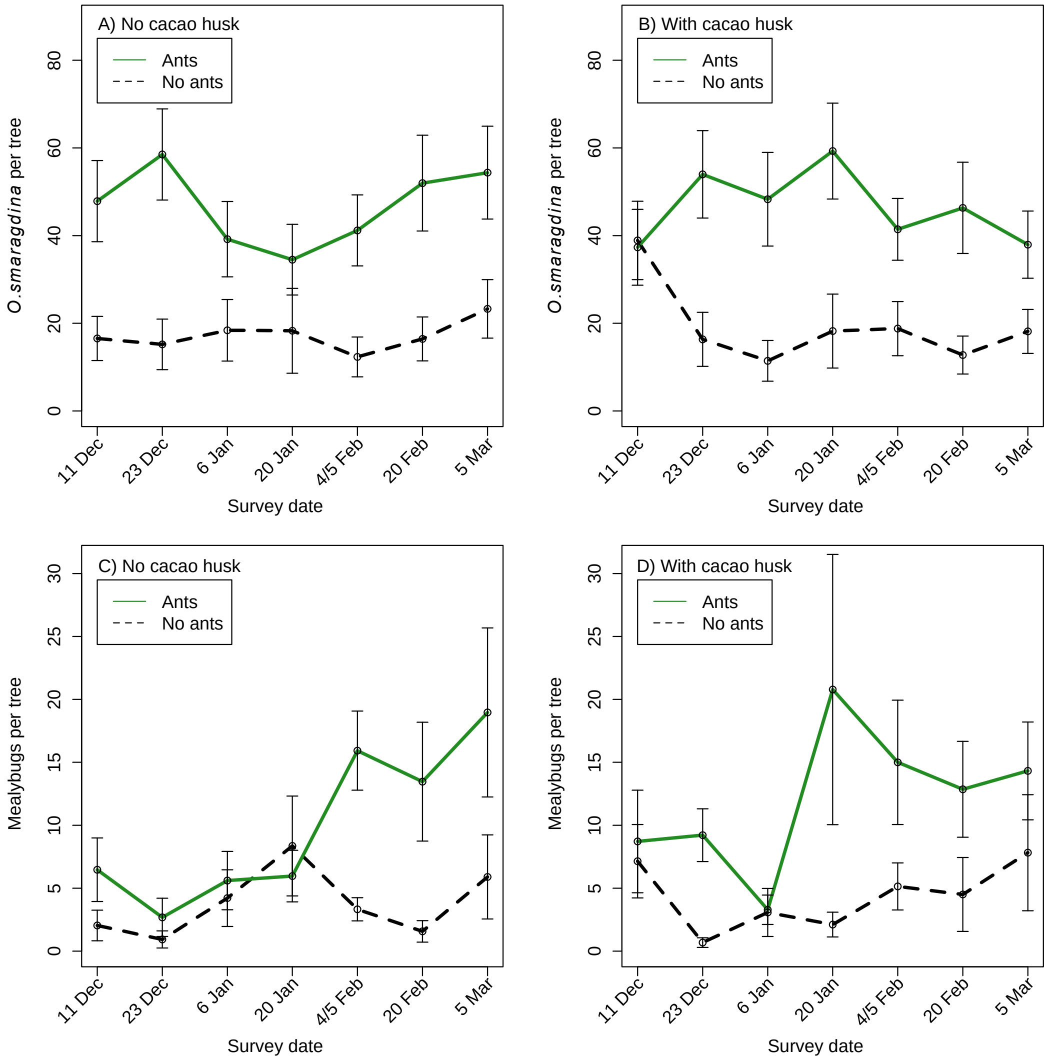
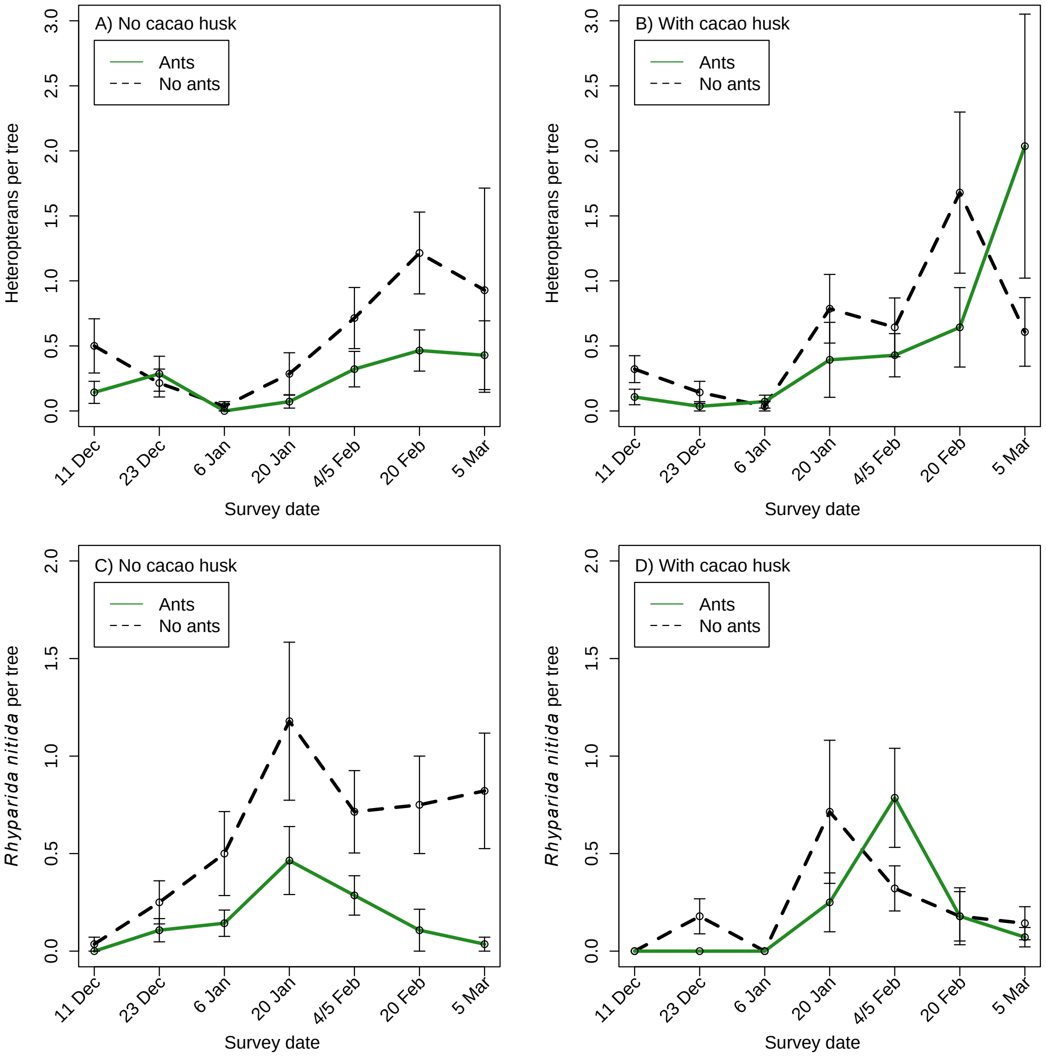

A) No cacao husk
B) With cacao husk
Ants
No ants
O.smaragdina per tree
0
20
40
60
80
C) No cacao husk
D) With cacao husk
Mealybugs per tree
0
5
10
15
20
25
30
11 Dec
23 Dec
6 Jan
20 Jan
4/5 Feb
20 Feb
5 Mar
Survey date

FIGURE 3.


A) No cacao husk
B) With cacao husk
C) No cacao husk
D) With cacao husk
Ants
No ants
Heteropterans per tree
Rhyparida nitida per tree
0.0
0.5
1.0
1.5
2.0
2.5
3.0
11 Dec
23 Dec
6 Jan
20 Jan
4/5 Feb
20 Feb
5 Mar
Survey date