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REVIEW

Ants as tools in sustainable agriculture

Joachim Offenberg*

Department of Bioscience, Aarhus University, Vejlsoevej 25, 8600 Silkeborg, Denmark

Summary

1. With an expanding human population placing increasing pressure on the environment, agriculture needs sustainable production that can match conventional methods. Integrated pest management (IPM) is more sustainable, but not necessarily as efficient as conventional non-sustainable measures.

2. Being predatory and organized as superorganisms, ants possess traits making them suitable agents in IPM. Recent works on weaver ants *Oecophylla* spp. showcase ants as highly efficient pest controllers. A synthesis shows that weaver ants can reduce pest numbers and their damage and increase yields in multiple crops. Their efficiency is comparable to chemical pesticides or higher, while at lower costs. They provide a rare example of documented efficient conservation biological control.

3. Weaver ants share beneficial traits with almost 13 000 other ant species and are unlikely to be unique in their properties as control agents. A synthesis of applied work on other ant species illustrates potentials for control of arthropod pests, weeds and plant diseases in orchards, forestry and arable crops.

4. *Synthesis and applications*. By showing that ant biocontrol can match synthetic pesticides in a wide setting of agricultural systems, this review emphasizes the potential of managing ants to achieve sustainable pest management solutions. The synthesis suggests future directions and may catalyse a research agenda on the utilization of ants, not only against arthropod pests, but also against weeds and plant diseases. Lastly, it may stimulate implementation of already proven ant-based integrated pest management techniques.

Key-words: ants, conservation biocontrol, ecosystem service, food security, integrated pest management, Oecophylla

Introduction

In a world with a rapidly expanding population of increasingly wealthier people, there is growing demand for food and a simultaneous need for higher environmental sustainability. The area available for agricultural production is limited, and sustainable methods that do not compromise yields are needed (Finn 2013). Assistance to realize this goal may, unexpectedly for many, come from ants. Theoretical reflections and empirical data suggest the utilization of ants in integrated pest management (IPM) can foster sustainable yields in agricultural systems and, in some systems, at lower costs than alternative non-sustainable methods based on chemical pesticides.

Being organized as superorganisms, many ant species hold desirable characteristics unshared by most other beneficials. Firstly, ants are extremely abundant in most ecosystems. They comprise at least one-third of all insect biomass and may equal the biomass of humans (Hölldobler & Wilson 2009). With such abundance, any fruitful interaction derived from this taxon holds a high potential. Secondly, ants possess features making them suitable for biological control programmes (Risch & Carroll 1982). (i) Using recruitment systems based on trail laying, tandem running and alarm pheromones, ants recruit nest mates to high prey densities. Consequently, they show fast numerical responses when pest populations escalate. Recruitment behaviour can, moreover, be utilized to attract ants to focal points where their services are most needed (Maňák *et al.* 2013). (ii) Most ant species are polyphagous, cooperative and often with polymorphic worker forces, enabling them to deploy a wide range of prey types. They may exert pressure on several pest species and life stages; small workers may handle eggs, whereas larger workers may engage larger sized individuals. (iii) On top of this,

*Correspondence author. E-mail: joaf@bios.au.dk

their territorial behaviour makes them attack and deter pests that are far beyond the size of potential prey. For example, African elephants *Loxodonta africana* avoid feeding on acacias *Vachellia drepanolobium* associated with symbiotic ants (Goheen & Palmer 2010). (iv) Ants are able to store protein in the form of trophic eggs and brood that may be cannibalized (Nonacs 1991), making their colonies stable and a predictable service with low management costs. Rueppell & Kirkman (2005) showed that colonies of *Temnothorax rugatulus* survived 8 months without food. (v) Lastly, this latter behaviour also means that colonies show high prey satiation levels. At high prey densities, ants continue to forage beyond the limits of other arthropods, as they may utilize prey to build up populations of larvae and trophic eggs. Thus, ants can exert continued pressure on pests even after prolonged periods with high pest densities.

With these attributes, ants have started to attract attention as control agents against a number of pests in different agricultural systems; especially, work on weaver ants *Oecophylla smaragdina* and *O. longinoda* has accumulated (Fig. 1). Empirical work on these ants provides some of the first examples of well-documented cost-efficient conservation biological control (CBC) programmes, where conservation leads not only to more natural enemies, but also to cascading effects ultimately leading to increased yields. Here, I review recent work on weaver ants to illustrate their potential for a sustainable production of agricultural yields. I further argue that weaver ants are unlikely to be unique in their abilities to provide effective pest protection. Of the almost 13 000 described ant species, many other species are likely to hold similar properties. The well-studied weaver ant example, though, highlights the prospects of ant-based pest control. Weaver ant biology has been reviewed earlier starting with Way & Khoo's (1992) technical review unravelling the earliest scientific studies on weaver ant biocontrol. This work was followed by a review by Van Mele (2008) focusing on the research history of weaver ants placed in a political and market context. Following these reviews, a growing number of applied studies have been added to the literature (Fig. 1), leaving a need for a synthesis of recent work.

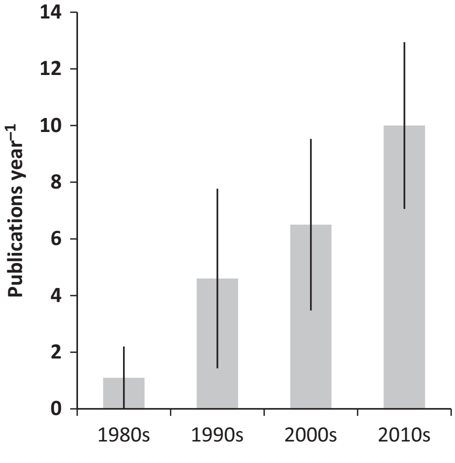

Fig. 1. The yearly (mean ± SD) number of applied weaver ant publications by decade found by Web of Science's search engine. Search criteria: Title = Oecophylla; Topic = biological control; Research domain = Science Technology. Search performed 1 February 2015. The 2010s include the years 2010–2013.

Managing weaver ants

Weaver ants are arboreal and build woven leaf nests in canopies of trees and shrubs and may control pest insects in plantations and forestry. To obtain sufficient pest control, it is often necessary to manage the ants to increase their density beyond natural levels. In brief, measures to support the ants are relatively simple and may include one or more interventions: (i) modifying or limiting use of insecticides, (ii) transplanting ant colonies into plantations, (iii) providing intra-colony host tree connections (with rope, poles or lianas), (iv) pruning trees to reduce fighting between neighbouring colonies, (v) providing supplementary ant feeding (sugar, water and sometimes protein) during parts of the season, (vi) providing artificial nesting sites to the ants (Offenberg 2014b) and (vii) limiting the action of competing ant species, for example by avoiding clean weeding under host trees, by applying sticky barriers around tree trunks or by chemically or physically controlling undesired species (Seguni, Way & Van Mele 2011). Using these low cost measures, ants can be maintained in mono-crop plantations in most systems, though mixed cropping will further facilitate ant populations and is a prerequisite in a few cases (Seguni *et al.* 1999; Peng, Christian & Reilly 2009). Kept at high densities, weaver ants may benefit plant production by (i) preying on pest insects, (ii) deterring pests physically (Way & Khoo 1992) or (iii) deterring them chemically (Offenberg 2014a).

It is a 'low-tech, low cost' methodology. What is needed is know-how on weaver ant management, a piece of rope or liana and a pruner. This allows even the most resource poor farmers and growers to adopt the technology, given they are informed about its existence and trained in its use. An investment in time rather than cash is especially marketable in developing countries, where salaries are low. Here, the weaver ant technology may be the only option, as shortage of cash prevents farmers from purchasing more expensive solutions.

Feasibility of weaver ant biocontrol

In a journal issue devoted to the progress of CBC, the scarcity of studies documenting trophic effects on pest populations and crop yields was addressed; ideally also including cost-benefit studies comparing CBC with other control systems (Cullen *et al.* 2008; Griffiths *et al.* 2008; Jonsson *et al.* 2008). Such studies were claimed to be rare, if existing at all, but are, nevertheless, needed before CBC programmes are adopted by farmers. Apparently unnoticed, a review of recent weaver ant biocontrol reveals systems with well-documented trophic cascades, methodological competitiveness and cost efficiency (Table 1). Studies are in the following divided into (i) studies documenting top-down effects from ants to crop yields, (ii) studies that additionally compared weaver-ant-CBC with alternative control systems and, lastly, (iii) studies considering the economics of weaver-ant-CBC by comparing costs and benefits with pesticide-based control systems.

Top-down effects

A number of studies show cascading effects from ants to pests, pest damage and crop yields. Olotu *et al.* (2013) compared mirid and coreid bug damage on Tanzanian cashew trees with and without weaver ant nests *O. longinoda* and found that the percentage of shoots damaged by *Helopeltis* sp. decreased from 33% on control trees without ants to 6·2% on trees with ant nests. Similarly, nut damage caused by *Pseudotheraptus wayi* decreased from 23·5% to 4·3%. In Malaysian oil palms, Pierre & Idris (2013) investigated the effect of *O. smaragdina* on herbivore damage caused by the bagworm *Pteroma pendula*. Ants preyed on bagworms, leading to fewer bagworms on ant-associated palms and much less damage compared to palms without ants. In the former group, 91·3% of palms were healthy without foliar injury, whereas only 1·8% of the palms without ants were healthy. Also, fruit productivity was higher on ant–palms. In Punjab in India, Bharti & Silla (2011) compared mango and citrus (species/variety not provided) yields between trees with and without *O. smaragdina* nests. They found that trees with ant nests produced 18% and 20% higher yields than trees without nests in mango and citrus, respectively.

Top-down effects are also found in forestry. Peng and co-workers tested the feasibility of weaver-ant-CBC on African mahogany *Khaya senegalensis*:Meliaceae in North Australia over a 3-year period on six different sites. The ants were, via predation on immature stages and physical deterrence of adults, able to control all major pests, including shoot borers *Hypsipyla robusta*, fruit spotting bugs *Amblypelta lutescens*, yellow loopers *Gymneoscelis* sp. and bush crickets *Myara yabmanna* (Peng, Christian & Reilly 2011, 2012, 2013). The main problem was the development of multiple leaders caused by insect attacks that made trees lose their value as timber. Compared to treatments without ants, trees in the ant treatments produced 40% fewer multiple leaders (Peng, Christian &

Table 1. Documentation level of weaver ant biocontrol efficiency by crop and country. Grey areas show the levels to which each case was tested and +, − and n indicate desired, undesired and neutral effects, respectively (in favour of weaver ant biocontrol). The first three levels indicate trophic levels, the fourth level indicates whether weaver ant biocontrol was compared to other control methods, and the fifth level indicates whether these comparisons were accompanied by economic cost-benefit analyses. Detected higher level effects were assumed to be preceded by lower level effects, even if lower levels were not tested directly. The last row in the table shows column totals with desirables (+) in parentheses. For example, out of 17 studies investigating nine crops in eight countries, six studies included cost-benefit analyses of which four found ant biocontrol superior to tested alternatives

		Levels affected					
Crop	Country	Pest reduction	Damage reduction	Yield increase	Comparison to alternatives	Cost-benefit analysis	Reference
Cashew	Tanzania	+	+				Olotu *et al.* (2013)
	Ghana	+	+	+	+		Dwomoh *et al.* (2009)
	Benin*	+	+	+	+		Anato *et al.* (2015b)
	Australia	+	+	+	+	+	Peng, Christian & Gibb (2004)
	Ghana†	+	+	+	+	+	Aidoo (2009)
Citrus	India	+	+	+			Bharti & Silla (2011)
	Thailand	+	+	+	n	n	Offenberg, Cuc & Wiwatwitaya (2013)
	Vietnam	+	+	+	n	+	Offenberg, Cuc & Wiwatwitaya (2013)
Mango	India	+	+	+			Bharti & Silla (2011)
	Australia	+	+	+	+	+	Peng & Christian (2005)
	Thailand	–	–	–	–	–	Offenberg, Cuc & Wiwatwitaya (2013)
Cocoa	Ghana	+	+	+	–		Ayenor *et al.* (2007)
Oil palm	Malaysia	+	+	+			Pierre & Idris (2013)
African Mahogany	Australia	+	+	+			Peng, Christian & Reilly (2009–2013)
Red Cedar	Australia	+	+				Peng, Christian & Reilly (2009)
Hopea odorata	Vietnam	+	+				Vu, Eastwood & Burckhardt (2012)
Pongamia pinnata	India	+	+				Hosetti & Rudresh (2012)
Totals							
9	8	17 (16)	17 (16)	13 (12)	9 (7)	6 (4)	17

*Only different weaver ant treatments were compared. †Data on costs and net returns were not provided in the article.

Reilly 2009), and the percentage of trees with pest-caused multiple leaders was more than ninefold higher in control treatments (Peng, Christian & Reilly 2010). Economic assessments estimated that the use of ants would increase timber production with 40%, corresponding to an increased income of 49 600 AUD ha^{-1} for a 20-year rotation (Peng, Christian & Reilly 2009). The costs of ant management were not assessed, but considered unlikely to exceed benefits despite mahogany needs protection when trees are still too small to host weaver ants, and management, therefore, involves (i) planting of acacia host trees between mahogany seedlings, (ii) transplantation of ant colonies, (iii) connecting acacia hosts with mahogany seedlings by lines and (iv) the provision of ant food. The effect of ants was also tested on red cedar *Toona ciliata* shoot borers *H. robusta* during these studies (Peng, Christian & Reilly 2009). The presence of ants significantly reduced the amount of shoot borer damage compared to cedar seedlings without ants, especially if ants were combined with a physical barrier around the growing tip used to reduce borer attacks. Despite a significant damage reduction, damage still reached 70%, which was above the economic injury level and, therefore, not acceptable to growers. The density of ants needed for effective protection was considered difficult to achieve under field conditions. Interestingly, it was found that a water-based extract made from ants and sprayed on seedlings was able to deter shoot borer females from egg laying, however, only for 1–2 days, which was too short for extracts to be practically feasible. In Vietnam, Vu, Eastwood & Burckhardt (2012) studied the damage caused by the psyllid pest *Trioza hopae* on its timber host tree *Hopea odorata*. They found that *O. smaragdina* preyed on psyllids, and pest damage on mature trees was negatively correlated with the presence of the ants. In Karnataka in India, Hosetti & Rudresh (2012) observed that *O. smaragdina* preyed on the pentatomid bug *Cyclopelta siccifolia* on *Pongamia pinnata* trees. Bug numbers were from 4·5 to 5·5 times lower on trees with abundant weaver ants compared to trees without ants and, accordingly, bug damage was from 4·1 to 4·5 times lower on the ant trees.

Ants versus alternative control measures

Apart from documenting trophic effects, a number of studies have compared the use of weaver ants with other types of pest control. In Ghanaian cashew, Dwomoh *et al.* (2009) compared the use of *O. longinoda* with two chemical insecticide treatments (cypermethrin+dimethoate and lambda-cyhalothrin) and a control treatment (water). They found pest damage was negatively correlated with the number of weaver ant nests and trees in the ant and the two chemical treatments had <6% pest damage on shoots, panicles and fruits, while water-sprayed control trees showed damage as high as 37·8%. The abundance of three sap sucking bugs (*Helopeltis schoutedeni, Pseudotherapthus devastans* and *Anoplocnemis curvipes*) was more than fourfold lower in the ant and chemical treatments compared with the control treatment and, correspondingly, nut yields were significantly and more than four times higher in ant and chemical treatments. There was no significant difference in yields between ant and chemical treatments. In a 2-year study in Beninese cashew, weaver ants alone, weaver ants fed sugar and weaver ants in combination with an application of spinosad (IPM) were contrasted with a control treatment. Ants, ants fed sugar and ants in the IPM treatments, respectively, produced yields that were 78%, 122% and 151% higher than the control treatment (Anato *et al.* 2015b). Surprisingly, the percentage of nuts with thrips damage was higher in the ant treatments, though absolute numbers of first class nuts and yields were also higher. In a 3-year study in Ghanaian cocoa, the effect of *O. longinoda* was contrasted with the use of mass trapping by a sex pheromone, the application of neem extract *Azadirachta indica* and a control treatment (Ayenor *et al.* 2007). Mean number of pest capsids was lowest in the weaver ant treatment, which was significantly lower than the control (2·4 times) and the neem treatment (2 times), but not different from the pheromone trapping treatment (1·2 times). The damage inflicted by capsids (mainly *Sahlbergella singularis* and *Distantiella theobroma*) on the trees showed a similar pattern. In 1 of 3 years, the study detected significantly higher yields (70%) in the ant treatment compared with the control. In comparison, the neem and pheromone trapping treatments produced higher yields than the control in 2 of 3 years. All three treatments were compatible and may be combined in IPM approaches.

Economic returns

As the weaver ant technology can compete in efficiency with other systems, its economic viability depends on its costs. The main cost of weaver ant biocontrol is the time invested in the transplantation of ant colonies from natural habitats into plantations and, if required, the time spent on feeding the ants. Thus, costs depend on salaries. In Thailand and Vietnam, first-year transplantation costs were 0·28 and 0·27 USD tree^{-1}, respectively, with costs increasing approximately 4- to 6-fold if ant feeding was practiced (Offenberg, Cuc & Wiwatwitaya 2013). In Northern Australia, the average cost of transplanting weaver ants in cashew was 201 AUD hectare^{-1} year^{-1} ($\approx$2 AUD tree^{-1}) over a 4-year period (Peng, Christian & Gibb 2004). The average yearly cost of using weaver ants in mango in combination with soft chemicals (see below) was 3·23 AUD per tree over a 3-year period (Peng & Christian 2005). As seen below, these costs are lower than application of insecticides and the difference only increases when consolidated costs of insecticides are included as, for example, costs on human health.

The first studies to document economic feasibility of weaver-ant-CBC were published by Peng and co-workers in 2004 and 2005 based on work in cashew and mango plantations in Northern Australia. In cashew, Peng, Christian & Gibb (2004) found that not only were weaver ants more efficient in controlling all major pests, but also the technology was cheaper than using chemical insecticides. Despite high costs of the weaver ant technology during the first year where ant colonies were transplanted (colonies persist for 3 years on average), the cost of the ant technology over 4 years was only 43% of the cost of using chemicals. At the same time, yields in ant plots were 49% higher, leading to an increased net income of 71%.

In mango, *O. smaragdina* was able to control most pests, except mealybugs (Peng & Christian 2005). Therefore, ants were combined with the use of 'soft' chemicals (1·5% potassium soap and 2% white oil) in an IPM treatment. These chemicals reduced mealybug infestations below the economic injury level without detrimental effects on ants. This IPM approach was compared to chemical insecticides. Over three cropping seasons, the IPM treatment produced 25% higher yields, however, with only a single season showing a significantly higher yield (14%). A more pronounced effect was found on fruit quality. Overall, the IPM treatment produced 45% more first class fruits, and the difference was significant in two of three seasons, with increases in premium quality of 211% and 53%, respectively. As mango price was highly dependent on fruit quality, net income over the three seasons was 73% higher in the IPM treatment, despite the fact that it was slightly lower in the first year, where weaver ant costs were high due to the labour involved in transplanting ant colonies. Overall, the cost of the IPM treatment was 7% lower than the cost of insecticides.

In Thailand and Vietnam, Offenberg, Cuc & Wiwatwitaya (2013) contrasted profits between *O. smaragdina* and chemically protected plots in citrus and mango. In Thai pomelo and Vietnamese mixed citrus (pomelo and orange), ants and chemical insecticides led to equal fruit yields. However, lower costs in ant treatments generated profit gains of 15 and 47%, respectively, in ant plots compared with insecticide treated plots; only the 47% gain in the Vietnamese plantation was statistically significant. The higher gains achieved with ants in Vietnam were the result of high costs related to insecticide sprayings, as local practice suggested 11 applications year^{-1}. In contrast, in mango in Thailand ant protection was ineffectual against leafhoppers. Here, the profit in ant plots was negative and 125% lower than in insecticide plots. The lack of protection in ant plots was caused by the ant-attended leafhopper *Idioscopus clypealis* destroying mango flowers in the weaver ant treatment. In that case, an IPM approach may have led to better protection.

Lastly, in a short note Aidoo (2009) described Ghanaian cashew tree health and yields to be higher in plantations using *O. longinoda* compared to plantations using insecticides. Aidoo (2009) also claimed that because management with weaver ants was cheaper than applying chemicals, net returns increased. However, no data was provided to support this claim.

Disadvantages (and their solutions)

Weaver ants show high potential; however, the technology also faces challenges. Some farmers are reluctant to use weaver ants, as they attack not only pests but also humans. A number of ways to reduce the nuisance from ants have been reviewed by Van Mele *et al.* (2009). Wearing beekeeper protective clothing or the application of fine powder (e.g. cassava flour or wood ash) on hands and feet will reduce attacks from worker ants. Also, spraying of water will inactivate the ants for a while and allow a less painful fruit harvest. Furthermore, as a positive perception of the ants advances in concert with experienced benefits, tolerance increased among stakeholders.

Ants may attack other beneficial organisms; for example, they may deter pollinators. Tsuji *et al.* (2004) found that the presence of *O. smaragdina* in rambutan *Nephelium lappaceum* flowers significantly decreased visiting rates of flying insects, including the major pollinator *Trigona minangkabau;* however, the effect on fruit set was not assessed. In contrast, Pierre & Idris (2013) did not find negative effects of *O. smaragdina* on the major pollinator *Elaeidobius kamerunicus* of oil palms, as the ants did not attack the beetles. Counter-intuitively, weaver ants preying on pollinators may end up benefitting flower reproductive success. Gonzalvez *et al.* (2013) found that *Melastoma malabathricum* flowers produced weaver ant attractants and the ants increased flower reproduction, since they facilitated visits from a more effective pollinator by preying selectively on a less effective species. Only the less effective species could be caught by the ants.

Weaver ants engage in trophobiotic mutualisms with attended hemipterans. In this interaction, they act indirectly as herbivores, since the honeydew they collect ultimately derives from the host trees. As such, trees bear costs, yet weaver ants also prey on trophobionts for protein when their demand for carbohydrates is fulfilled, which may reduce plant costs (Way 1954). In fact, attended homopterans may increase plant fitness, as they often inhabit and attract ants to the most vulnerable plant tissues, such as developing shoots, flowers and fruits. Here, the ants collect honeydew, but simultaneously prey or deter pest insects, leading to a net benefit for the plant. Reviewing 30 studies on outcomes of ant–hemiptera–plant interactions, Styrsky & Eubanks (2007) found that in 73% of these studies, plants experienced net benefits from indirect effects rather than a cost. In other words, associations between weaver ants and hemipterans are not necessarily harmful. Further, weaver ants have been shown to attend mainly non-pest hemipterans, for example Stictococcidae (Kenne *et al.* 2003). Yet, trophobioses deserve attention, and cases exist where combinations of weaver ants with other IMP measures are needed to control hemipteran pests (Peng & Christian 2005).

During nest building, weaver ants bend leaves out of their original position, imposing mechanical stress to leaf petioles. This inflicts costs by decreasing leaf longevity and photosynthesis. *R. mucronata* leaves used in ant nests suffered more than five times higher rates of premature leaf loss compared with control leaves not used in nests. On the other hand, only 0·25% of the leaves on ant trees were used in ant nests, and the associated costs were estimated to be 6–20 times lower than the benefits gained via a decreased leaf area removed by herbivores (Offenberg *et al*. 2004, 2006). Similarly, nest leaves on Benin mango showed reduced leaf longevity, but the number of leaves used in nests was only between 0·42% and 1·2% (Anato *et al*. 2015a). Thus, nests are detrimental to the leaves used in the construction; however, such leaves constitute a minor fraction of the tree's total foliage, and negative effects seem to be minimal.

Beyond weaver ants

Weaver ants provide the most well-documented example of ant-based agricultural pest management; however, their positive attributes are not unique and a multitude of other ant species are likely to show similar effectivity in crop protection (Rico-Gray & Oliveira 2007).

Extensive investigations for more than a decade in Mexican coffee have shown Azteca ants *Azteca instabilis* to possess a keystone role in a highly complex network of direct and indirect effects between ants, insect natural enemies, herbivores, pathogenic fungi and coffee. Spatial dynamics of these populations and their lower and higher order interactions lead to ecological homeostasis and prevent outbreaks of four potential coffee pests: the coffee berry borer *Hypothenemus hampei*, the coffee rust disease *Hemileia vastatrix*, a leaf miner *Leucoptera coffeella* and the green coffee scale *Coccus viridis* – species known as coffee pests from other areas. This system have been reviewed by Vandermeer, Perfecto & Philpott (2010) and Hsieh & Perfecto (2012). Further, Gonthier *et al*. (2013) showed that six out of eight tested ant species were able to reduce coffee berry borer damage. In Martinique banana plantations, *Solenopsis geminata* and *Camponotus sexguttatus* have been suggested as biocontrol agents against the banana weevil *Cosmopolites sordidus* (Mollot *et al*. 2012, 2014). Predation on weevil eggs increased from 8% to 70% when the density of *S. geminata* increased approximately fivefold via the addition of a cover crop in the plantation. In a Colombian passionfruit plantation, the pest flies *Dasiops* spp. was attacked by ants when entering the soil for pupation. During burrowing, 12·5% of the fly larvae were eaten by ants (mainly *Pheidole* spp. and *Solenopsis* spp.), while subsequent pupae mortality was 75%, and also ascribed to ants as they comprised 80% of the soil predators (Carrero *et al*. 2013). In peach *Prunus persica* in USA, ants were crucial in reducing the oriental fruit moth *Grapholita molesta* in its larvae and pupal stages (Mathews, Bottrell & Brown 2011). However, the ants also antagonized the egg parasitoid *Trichogramma minutum*.

Examples are also found in forestry and annual crops. Pine weevil *Hylobius abietis* (L.) damage on coniferous seedlings in Sweden was reduced with one-third by attracting *Formica* and *Myrmica* spp. to seedlings with sugar baits (Maňák *et al*. 2013). Oliveira *et al*. (2012) suggested *Solenopsis saevissima, Crematogaster* sp. and *Pheidole* sp. as important predators of sugar cane borers *Diatraea saccharalis* in Brazilian sugarcane, as they fed on eggs and immatures of this pest. Honduran maize production suffers from attacks by the fall armyworm *Spodoptera frugiperda* which is partly kept at bay through action of ants, social wasps, carabid beetles and spiders (Wyckhuys & O'Neil 2010). In cotton, peanut and soya bean, the southern green stink bugs *Nezara viridula* may be controlled by *Solenopsis invicta* as egg mortality of up to 80% was caused mainly by these ants (Olson & Ruberson 2012). Also, mites may be controlled by ants. The survival of spider mites *Tetranychus kanzawai* feeding on bean leaves was reduced by more than 60% if *Pristomyrmes punctatus* ants acted in concert with predatory mites *Neoseiulus womersleyi* that chased the spider mites out of their protective webs leaving them vulnerable to ant attacks (Otsuki & Yano 2014). Lastly, weed control may be afforded by seed harvester ants *Messor barbarus* that remove up to approximately 80% of artificially placed weed seeds (*Lolium multiflorum, Vicia villosa*) in Spanish barley and wheat fields (Baraibar *et al*. 2009).

These recent publications provide ample evidence of ant species that bear potential to be utilized in crop protection. Even more convincingly, numerous plant species have developed ant attractants in the form of extrafloral nectaries, domatia and food bodies to support ants and in this way pay for protection. In a meta-analysis ($N = 273$ studies), Rosumek *et al*. (2009) found that ant–plants on average suffered reductions of 24–52% in fitness parameters, when their ants were removed.

Future directions

Some ant species work well in protecting particular cropping systems, whereas others are harmful and yet others play dual roles. A future challenge is to identify positive and negative ant–crop matches and to develop management facilitating the positives and eliminating the negatives. For example, Trible & Carroll (2014) found that the presence of *S. geminata* suppressed beneficial ant species that were the primary predators of coffee berry borers. The removal of *S. geminata* increased the removal rate of borers almost fourfold; elimination of this ant may increase the efficiency of ant biocontrol. Alternatively, harmful species may be spatially manipulated, as they can serve positive roles in parts of the cropping system. When *P. megacephala* and *Anoplolepis custodiens* that tended pest hemipterans in citrus were excluded from the canopy by sticky barriers, they were forced to forage in the soil where they significantly reduced the survival of soil dwelling pests (Bownes, Moore & Villet 2014). Thus, in some cases spatial management of a species may work better than its elimination. Other techniques suggested to facilitate abundance of beneficials at the cost of detrimental ant species have been shade management in, for example, coffee (Pardee & Philpott 2011) and cocoa (Tadu *et al.* 2014) and manipulation of ant mosaics as first presented by Majer (1976).

Facilitating single species of ants may not necessarily be the best solution, as higher ant diversity may improve ecosystem functioning via complementary effects of multiple predatory species and via dilution of potential disservices of dominant species (Philpott & Armbrecht 2006; Wielgoss *et al.* 2014). Diverse ant communities may thus provide protection against a wider range of pests and increase yields. Wielgoss *et al.* (2014) found that introduction of a dominant invasive ant (*Philidris* cf. *cordata*) into Indonesian cocoa plantations decreased ant diversity and evenness and resulted in 34% lower yields compared with unmanipulated control plots. In comparison, ant excluded plots led to 27% reductions in yield. Managements known to increase ant diversity are conservation of natural habitats, reduced use of pesticides, less intensive tilling and conservation of shade trees (Peck, McQuaid & Campbell 1998; Kenne *et al.* 2003; Perfecto, Vandermeer & Philpott 2014). The effects of ant diversity on pest control need future attention.

As ants attend potentially harmful trophobionts, it is relevant to ask whether some crops are more likely to suffer from such associations than others. Only little work has been done to elucidate general patterns. Arboreal ants hosted by perennial plants may be less likely to attend pest hemipterans than ground-nesting ants (Kenne *et al.* 2003). Thus, perennial crops may be less prone to harmful trophobioses compared to annuals that are mainly visited by ground ants. An explanation could be that arboreal ants are selected against engagement with harmful trophobionts, as they share fitness with the host plants on which they nest. If attending harmful hemipterans, ants indirectly deteriorate their host plant and nesting opportunity. This is not the case with ground-nesting ants. Whether this has any implications for the benefits derived from native versus invasive ants remains speculative at present. It may be argued that invasive ants (e.g. *P. megacephala* and *Paratrechina longicornis*) tend to attend pest hemipterans (Kenne *et al.* 2003; Bownes, Moore & Villet 2014). However, as described above several cases exist where ground-nesting invasive ants act as beneficials even in annual crops (see also Kaplan & Eubanks 2005). Thus, more work is needed to identify general patterns among these associations.

No ant species will become a global solution to all pest assemblages in any particular crop. Finding IPM measures that can supplement ants and thus provide solutions applicable in a broader spectrum of ecological settings is important for a wider implementation of ant biocontrol, as the uncertainty resting with non-global solutions is likely to divert attention to more robust, but in many cases also less sustainable, solutions. Apart from identifying beneficial ant species/assemblages and developing techniques to optimize their impact, two recently discovered areas within applied myrmecology hold potential in future pest management.

As ants mark their territories chemically and use pheromone communication, an opportunity to evade their presence exists if this communication is eave-dropped by prey species. A mini review found that chemicals deposited by four out of five tested ant species were able to repel herbivorous insects, including fruit flies in mango (Offenberg 2014a). If pest species are able to detect semiochemicals deposited by ants, it may open a possibility to deter pests via artificially produced ant pheromones. However, whether the repelling properties of ant pheromones are a general phenomenon needs further research efforts. If so, chemical identification of the responsible compounds should be addressed.

Ants live in dense societies, and to combat diseases, they produce antibiotic compounds in glands or via fungal and bacterial symbionts. These compounds may end up on plant tissue and potentially protect plants against diseases. Several plant species associated with ants have shown less microbial pathogen loads and less damage inflicted by fungi and bacteria when ant partners were present compared to plants where ants were removed (see González-Teuber, Kaltenpoth & Boland 2014 and references therein). Such plants displayed lowered activities in their own biochemical defences, for example reduced chitinase levels, suggesting a co-evolution between ants and plants (Heil *et al.* 1999). Ants may also graze on pathogen spores (Letourneau 1998). Whether ants provide additional ecosystem services by providing indirect protection against diseases awaits further scrutiny that may provide a deeper understanding of ant–plant mutualisms and the basis for efficient utilization of this effect.

Conclusions

Weaver ants cause cascading effects to lower trophic levels, decreasing pest populations and their damage, successively resulting in higher crop yields. This is documented in several crops (Table 1). Further, these ants are comparable in efficiency with alternative control strategies, in some cases even leading to higher yields and at lower costs. As the use of weaver ants is sustainable, this ‘technology’ provides a rare example of sustainable production that matches conventional yields and is also a rare example of well-documented efficient CBC. Having said that, some potential disadvantages may follow; however, drawbacks may (i) be addressed via proper management (ant bites) or (ii) be of minor importance (the effect of ant nests). In other cases, (iii) what seems to be a problem at a first glance may turn out as the opposite (effects on pollinators and trophobiotic homopterans). Regardless, as net benefits are found in most published studies, positive effects are likely to outweigh these negatives. There is no doubt that plants can benefit from patrolling ants, but at the same time there is no doubt that some ant species are harmful rather than helpful. Weaver ants serve as a positive thoroughly investigated example. Other less well-studied ant species are likely to show similar properties in other agricultural systems. The challenge is to find species that work well in a particular setting and subsequently to develop management facilitating their establishment and persistence. In addition, identification of IPM components compatible with beneficial ant species is needed to supplement their actions. Last, but not least, future prospects may lie within indirect chemical effects of ants on arthropod pests and diseases. These effects are promising and are avenues to be explored to further develop the use of ants in pest control. Increased efforts on the study of ant communities as biocontrol agents may facilitate the development of sustainability in agriculture.

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Data accessibility

Data have not been archived because this article does not contain data.

References

Aidoo, K.S. (2009) Boosting cashew production in Ghana. *Bees for Development*, **91**, 8–9.

Anato, F.M., Sinzogan, A., Adandonon, A., Hounlidji, X., Offenberg, J., Kossou, D.K. & Vayssieres, J.F. (2015a) Impact of African weaver ant nests [*Oecophylla longinoda Latreille* (Hymenoptera: Formicidae)] on mango [*Mangifera indica* L. (Sapindales: Anacardiaceae)] leaves. *Sociobiology*, **62**, 39–45.

Anato, F.M., Wargui, R., Sinzogan, A., Offenberg, J., Adandonon, A., Vayssieres, J.F. & Kossou, D.K. (2015b) Reducing losses inflicted by insect pests on cashew, using weaver ants as efficient biological control agent. *Agricultural and Forest Entomology*, **17**, 285–291.

Ayenor, G.K., Van Huis, A., Obeng-Ofori, D., Padi, B. & Roeling, N.G. (2007) Facilitating the use of alternative capsid control methods towards sustainable production of organic cocoa in Ghana. *International Journal of Tropical Insect Science*, **27**, 85–94.

Baraibar, B., Westerman, P.R., Carrión, E. & Recasens, J. (2009) Effects of tillage and irrigation in cereal fields on weed seed removal by seed predators. *Journal of Applied Ecology*, **46**, 380–387.

Bharti, H. & Silla, S. (2011) Notes on the life history of *Oecophylla smaragdina* (Fabricius) and its potential as biological control agent. *Halteres*, **3**, 57–64.

Bownes, A., Moore, S.D. & Villet, M.H. (2014) My enemy's enemies: recruiting hemipteran-tending generalist ants for biological control in citrus orchards by spatial partitioning of foraging webs. *African Entomology*, **22**, 519–529.

Carrero, D.A., Melo, D., Uribe, S. & Wyckhuys, K.A.G. (2013) Population dynamics of *Dasiops inedulis* (Diptera: Lonchaeidae) and its biotic and abiotic mortality factors in Colombian sweet passionfruit orchards. *Journal of Pest Science*, **86**, 437–447.

Cullen, R., Warner, K.D., Jonsson, M. & Wratten, S.D. (2008) Economics and adoption of conservation biological control. *Biological Control*, **45**, 272–280.

Dwomoh, E.A., Afun, J.V.K., Ackonor, J.B. & Agene, V.N. (2009) Investigations on *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae) as a biocontrol agent in the protection of cashew plantations. *Pest Management Science*, **65**, 41–46.

Finn, J. (2013) Virtual issue: applied ecology in agricultural systems. *Journal of Applied Ecology* (http://www.journalofappliedecology.org/view/0/virtualissues/agroecologyvi.html).

Goheen, J.R. & Palmer, T.M. (2010) Defensive plant-ants stabilize megaherbivore-driven landscape change in an African savanna. *Current Biology*, **20**, 1768–1772.

Gonthier, D.J., Ennis, K.K., Philpott, S.M., Vandermeer, J. & Perfecto, I. (2013) Ants defend coffee from berry borer colonization. *BioControl*, **58**, 815–820.

González-Teuber, M., Kaltenpoth, M. & Boland, W. (2014) Mutualistic ants as an indirect defence against leaf pathogens. *New Phytologist*, **202**, 640–650.

Gonzalvez, F.G., Santamaria, L., Corlett, R.T. & Rodriguez-Girones, M.A. (2013) Flowers attract weaver ants that deter less effective pollinators. *Journal of Ecology*, **101**, 78–85.

Griffiths, G.J.K., Holland, J.M., Bailey, A. & Thomas, M.B. (2008) Efficacy and economics of shelter habitats for conservation biological control. *Biological Control*, **45**, 200–209.

Heil, M., Fiala, B., Linsenmair, K.E. & Boller, T. (1999) Reduced chitinase activities in ant plants of the genus Macaranga. *Naturwissenschaften*, **86**, 146–149.

Hölldobler, B. & Wilson, E.O. (2009) *The Superorganism*. W. W. Norton & Company Inc, New York, NY, USA.

Hosetti, B.B. & Rudresh, B.S. (2012) Studies on *Oecophylla smaragdina* as a bio-control agent against pentatomid bug infesting on Pongamia tree. *Journal of Environmental Biology*, **33**, 1103–1106.

Hsieh, H.Y. & Perfecto, I. (2012) Trait-mediated indirect effects of phorid flies on ants. *Psyche*, Article number 380474.

Jonsson, M., Wratten, S.D., Landis, D.A. & Gurr, G.M. (2008) Recent advances in conservation biological control of arthropods by arthropods. *Biological Control*, **45**, 172–175.

Kaplan, I. & Eubanks, M.D. (2005) Aphids alter the community-wide impact of fire ants. *Ecology*, **86**, 1640–1649.

Kenne, M., Djiéto-Lordon, C., Orivel, J., Mony, R., Fabre, A. & Dejean, A. (2003) Influence of insecticide treatments on ant-hemiptera associations in tropical plantations. *Journal of Economic Entomology*, **96**, 251–258.

Letourneau, D.K. (1998) Ants, stem-borers, and fungal pathogens: experimental tests of a fitness advantage in Piper ant-plants. *Ecology*, **79**, 593–603.

Majer, J.D. (1976) The maintenance of the ant mosaic in Ghana cocoa farms. *Journal of Applied Ecology*, **13**, 123–144.

Maňák, V., Nordenhem, H., Björklund, N., Lenoir, L. & Nordlander, G. (2013) Ants protect conifer seedlings from feeding damage by the pine weevil *Hylobius abietis*. *Agricultural and Forest Entomology*, **15**, 98–105.

Mathews, C.R., Bottrell, D.G. & Brown, M.W. (2011) Interactions between extrafloral nectaries, ants (Hymenoptera: Formicidae), and other natural enemies affect biological control of *Grapholita molesta* (Lepidoptera: Tortricidae) on peach (Rosales: Rosaceae). *Environmental Entomology*, **40**, 42–51.

Mollot, G., Tixier, P., Lescourret, F., Quilici, S. & Duyck, P.F. (2012) New primary resource increases predation on a pest in a banana agroecosystem. *Agricultural and Forest Entomology*, **14**, 317–323.

Mollot, G., Duyck, P.F., Lefeuvre, P., Lescourret, F., Martin, J.F., Piry, S., Canard, E. & Tixier, P. (2014) Cover cropping alters the diet of arthropods in a banana plantation: a metabarcoding approach. *PLoS ONE*, **9**, e93740.

Nonacs, P. (1991) Less growth with more food: how insect-prey availability changes colony demographics in the ant, *Camponotus floridanus*. *Journal of Insect Physiology*, **37**, 891–898.

Offenberg, J. (2014a) Pest repelling properties of ant pheromones. *IOBC-WPRS Bulletin*, **99**, 173–176.

Offenberg, J. (2014b) The use of artificial nests by weaver ants: a preliminary field observation. *Asian Myrmecology*, **6**, 119–128.

Offenberg, J., Cuc, N.T.T. & Wiwatwitaya, D. (2013) The effectiveness of weaver ant (*Oecophylla smaragdina*) biocontrol in Southeast Asian citrus and mango. *Asian Myrmecology*, **5**, 139–149.

Offenberg, J., Havanon, S., Aksornkoae, S., Macintosh, D. & Nielsen, M.G. (2004) Observations on the ecology of weaver ants (*Oecophylla smaragdina* Fabricius) in a Thai mangrove ecosystem and their effect on herbivory of *Rhizophora mucronata* Lam. *Biotropica*, **36**, 344–351.

Offenberg, J., Nielsen, M.G., Macintosh, D., Aksornkoae, S. & Havanon, S. (2006) Weaver ants reduce the longevity of leaves used for nest construction in Rhizophora trees. *Biotropica*, **38**, 782–785.

Oliveira, R.F., Almeida, L.C., Souza, D.R., Munhae, C.B., Bueno, O.C. & Morini, S.C. (2012) Ant diversity (Hymenoptera: Formicidae) and predation by ants on the different stages of the sugarcane borer life cycle *Diatraea saccharalis* (Lepidoptera: Crambidae). *European Journal of Entomology*, **109**, 381–387.

Olotu, M.I., Plessis, H., Seguni, Z. & Maniania, N.K. (2013) Efficacy of the African weaver ant *Oecophylla longinoda* (Hymenoptera: Formicidae) in the control of *Helopeltis* spp. (Hemiptera: Miridae) and *Pseudotheraptus wayi* (Hemiptera: Coreidae) in cashew crop in Tanzania. *Pest Management Science*, **69**, 911–918.

Olson, D.M. & Ruberson, J.R. (2012) Crop-specific mortality of southern green stink bug eggs in Bt- and non-Bt cotton, soybean and peanut. *Biocontrol Science and Technology*, **22**, 1417–1428.

Otsuki, H. & Yano, S. (2014) Functionally different predators break down antipredator defenses of spider mites. *Entomologia Experimentalis et Applicata*, **151**, 27–33.

Pardee, G.L. & Philpott, S.M. (2011) Cascading indirect effects in a coffee agroecosystem: effects of parasitic phorid flies on ants and the coffee berry borer in a high-shade and low-shade habitat. *Environmental Entomology*, **40**, 581–588.

Peck, S.L., McQuaid, B. & Campbell, C.L. (1998) Using ant species (Hymenoptera: Formicidae) as a biological indicator of agroecosystem condition. *Environmental Entomology*, **27**, 1102–1110.

Peng, R.K. & Christian, K. (2005) Integrated pest management in mango orchards in the Northern Territory Australia, using the weaver ant, *Oecophylla smaragidina*, (Hymenoptera: Formicidae) as a key element. *International Journal of Pest Management*, **51**, 149–155.

Peng, R.K., Christian, K. & Gibb, K. (2004) *Implementing ant Technology in Commercial Cashew Plantations and Continuation of Transplanted Green ant Colony Monitoring*. pp. 1–72. Australian Government, Rural Industries Research and Development Corporation, Barton, Australian Capital Territory, Australia.

Peng, R., Christian, K. & Reilly, D. (2009) *Green Ants as Biological Control Agents in Agroforestry*. pp. 134. Rural Industries Research and Development Corporation, Canberra, Australia.

Peng, R., Christian, K. & Reilly, D. (2010) Weaver ants, *Oecophylla smaragdin*a (Hymenoptera: Formicidae), as biocontrol agents on African mahogany trees, *Khaya senegalensis* (Sapindales: Meliaceae), in the Northern Territory of Australia. *International Journal of Pest Management*, **56**, 363–370.

Peng, R., Christian, K. & Reilly, D. (2011) The effect of weaver ants *Oecophylla smaragdina* on the shoot borer *Hypsipyla robusta* on African mahoganies in Australia. *Agricultural and Forest Entomology*, **13**, 165–171.

Peng, R., Christian, K. & Reilly, D. (2012) Biological control of the fruit-spotting bug *Amblypelta lutescens* using weaver ants *Oecophylla smaragdina* on African mahoganies in Australia. *Agricultural and Forest Entomology*, **14**, 428–433.

Peng, R., Christian, K. & Reilly, D. (2013) Using weaver ants *Oecophylla smaragdina* to control two important pests on African mahogany *Khaya senegalensis* in the Northern Territory of Australia. *Australian Forestry*, **76**, 76–82.

Perfecto, I., Vandermeer, J. & Philpott, S.M. (2014) Complex ecological interactions in the coffee agroecosystem. *Annual Review of Ecology, Evolution, and Systematics*, **45**, 137–158.

Philpott, S.M. & Armbrecht, I. (2006) Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecological Entomology*, **31**, 369–377.

Pierre, E.M. & Idris, A.H. (2013) Studies on the predatory activities of *Oecophylla smaragdina* (Hymenoptera: Formicidae) on *Pteroma pendula* (Lepidoptera: Psychidae) in oil palm plantations in Teluk Intan, Perak (Malaysia). *Asian Myrmecology*, **5**, 163–176.

Rico-Gray, V. & Oliveira, P.S. (2007) *The Ecology and Evolution of Ant-Plant Interactions*. The University of Chicago Press, Chicago, IL, USA.

Risch, S.J. & Carroll, C.R. (1982) The ecological role of ants in two Mexican agroecosystems. *Oecologia*, **55**, 114–119.

Rosumek, F.B., Silveira, F.A.O., De, S., Neves, F., De, U., Barbosa, N.P. *et al*. (2009) Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. *Oecologia*, **160**, 537–549.

Rueppell, O. & Kirkman, R.W. (2005) Extraordinary starvation resistance in *Temnothorax rugatulus* (Hymenoptera, Formicidae) colonies: demography and adaptive behavior. *Insectes Sociaux*, **52**, 282–290.

Seguni, Z.S.K., Way, M.J. & Van Mele, P. (2011) The effect of ground vegetation management on competition between the ants *Oecophylla longinoda* and *Pheidole megacephala* and implications for conservation biological control. *Crop Protection*, **30**, 713–717.

Seguni, Z.S.K., Mwaiko, W., Materu, C. & Nyange, V. (1999) Effect of natural aerial crown connections between leaves and branches of coconut palms and interplanted citrus trees on interactions between *Pheidole megacephala* Fabricius and *Oecophylla longinoda* Latreille. *Tanzania Journal of Agricultural Sciences*, **2**, 107–113.

Styrsky, J.D. & Eubanks, M.D. (2007) Ecological consequences of interactions between ants and honeydew-producing insects. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 151–164.

Tadu, Z., Djiéto-Lordon, C., Yede, Youbi, E.M., Aléné, C.D., Fomena, A. & Babin, R. (2014) Ant mosaics in cocoa agroforestry systems of Southern Cameroon: influence of shade on the occurrence and spatial distribution of dominant ants. *Agroforestry Systems*, **88**, 1067–1079.

Trible, W. & Carroll, R. (2014) Manipulating tropical fire ants to reduce the coffee berry borer. *Ecological Entomology*, **39**, 603–609.

Tsuji, K., Hasyim, A., Harlion, & Nakamura, K. (2004) Asian weaver ants, *Oecophylla smaragdina*, and their repelling of pollinators. *Ecological Research*, **19**, 669–673.

Van Mele, P. (2008) A historical review of research on the weaver ant *Oecophylla* in biological control. *Agricultural and Forest Entomology*, **10**, 13–22.

Van Mele, P., Nguyen Thi Thu, C., Seguni, Z., Camara, K. & Offenberg, J. (2009) Multiple sources of local knowledge: a global review of ways to reduce nuisance from the beneficial weaver ant Oecophylla. *International Journal of Agricultural Resources Governance and Ecology*, **8**, 484–504.

Vandermeer, J., Perfecto, I. & Philpott, S. (2010) Ecological complexity and pest control in organic coffee production: uncovering an Autonomous Ecosystem Service. *BioScience*, **60**, 527–537.

Vu, N.T., Eastwood, R. & Burckhardt, D. (2012) Life history, damage assessment and control of *Trioza hopeae* (Hemiptera: Psylloidea), a serious pest on *Hopea odorata* (Malvales: Dipterocarpaceae) in Vietnam. *Entomological Research*, **42**, 11–18.

Way, M.J. (1954) Studies on the association of the ant *Oecophylla longinoda* (Latr) (Formicidae) with the scale insect *Saissetia zanzibarensis* Williams (Coccidae). *Bulletin of Entomological Research*, **45**, 113–134.

Way, M.J. & Khoo, K.C. (1992) Role of ants in pest-management. *Annual Review of Entomology*, **37**, 479–503.

Wielgoss, A., Tscharntke, T., Rumede, A., Fiala, B., Seidel, H., Shahabuddin, S. & Clough, Y. (2014) Interaction complexity matters: disentangling services and disservices of ant communities driving yield in tropical agroecosystems. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 1–10.

Wyckhuys, K.A.G. & O'Neil, R.J. (2010) Social and ecological facets of pest management in Honduran subsistence agriculture: implications for IPM extension and natural resource management. *Environment, Development and Sustainability*, **12**, 297–311.

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