Ants: Major Functional Elements in Fruit Agro-Ecosystems and Biological Control Agents

Lamine Diamé [1,2,*], Jean-Yves Rey [1,3,4], Jean-François Vayssières [3,4], Isabelle Grechi [4,5], Anaïs Chailleux [3,4,6] and Karamoko Diarra [2]

[1] Institut Sénégalais de Recherches Agricoles, Centre pour le Développement de l'Horticulture, BP 3120 Dakar, Senegal; jeanyvesp.rey@gmail.com

[2] Département de Biologie Animale, Université Cheikh Anta Diop de Dakar, BP 7925 Dakar, Senegal; karamoko.diarra@ucad.edu.sn

[3] Centre de Coopération Internationale de Recherche Agronomique pour le Développement, UPR HortSys, F-34398 Montpellier, France; jean-françois.vayssieres@cirad.fr (J.-F.V.); anais.chailleux@cirad.fr (A.C.)

[4] Centre de Coopération Internationale de Recherche Agronomique pour le Développement, University de Montpellier, HortSys, F-34398 Montpellier, France; isabelle.grechi@cirad.fr

[5] Centre de Coopération Internationale de Recherche Agronomique pour le Développement, UPR HortSys, F-97455 Saint-Pierre, La Réunion, France

[6] Biopass, Institut Sénégalais de Recherches Agricoles—University Cheikh Anta Diop de Dakar—Institut de Recherche pour le Développement, BP 2274 Dakar, Senegal

* Correspondence: diamelamine99@gmail.com

Abstract: Ants are a very diverse taxonomic group. They display remarkable social organization that has enabled them to be ubiquitous throughout the world. They make up approximately 10% of the world's animal biomass. Ants provide ecosystem services in agrosystems by playing a major role in plant pollination, soil bioturbation, bioindication, and the regulation of crop-damaging insects. Over recent decades, there have been numerous studies in ant ecology and the focus on tree cropping systems has given added importance to ant ecology knowledge. The only missing point in this knowledge is the reasons underlying difference between the positive and negative effects of ants in tree cropping systems. This review article provides an overview of knowledge of the roles played by ants in orchards as functional elements, and on the potential of *Oecophylla* weaver ants as biological control agents. It also shows the potential and relevance of using ants as an agro-ecological diagnosis tool in orchards. Lastly, it demonstrates the potential elements which may determine the divergent negative and positive of their effects on cropping systems.

Keywords: *Oecophylla* sp.; mango tree; *Citrus*; agroecosystem services

1. Introduction

Although ants are small and seemingly insignificant creatures as individuals, collectively, they are one of the dominant groups of the planet's animal biomass, accounting for around 10% [1]. They are countless and their importance comes as much from their number as it does from the social behavior associated with that number. They play a fundamental role in agro-ecosystem functioning and provide multiple services such as biological control [2], plant pollination [3], soil bioturbation [4,5], and bioindication [6], along with providing a diagnostic tool in orchards [7,8] or animal and plant biodiversity conservation [1]. The multiplicity of their roles is linked to the great diversity of their group compared to other animal taxa [6,9]. Ants play an important role in regulating crop-damaging insects. Some knowledge of their potential as biological control agents exists for certain species, particularly in horticulture [10–12]. That potential has been studied in the genus *Oecophylla*, whose ability to

control a wide range of insect pests has been demonstrated on crops such as citrus [13], mango [14] or cashew [15] in Africa, as well as citrus in tropical Asia and Australia [16]. Other genera such as *Azteca* [17,18], *Ectatomma* or *Wasmania* [19,20] also have been reported to be effective biological control agents. Ants also play an important role in plant pollination [3] and soil bioturbation [4,5]. Their effects on soil through aeration and chemical modifications as well as their relations with the other biotic components of agro-ecosystems such as plants, microorganisms and the other organisms in the soil are particularly significant.

Agro-ecology is defined as being an integrative discipline that brings about the synergism of agricultural, sociological and economic approaches [21]. Parameters such as the conservation and preservation of biodiversity are basic elements of agro-ecology. Thus, better resource management adopting an agro-ecological approach needs to focus on taking the whole biological component into account, along with the interactions between its elements [22]. Agro-ecologically speaking, management of ants in tree cropping systems requires knowledge of their positive and negative impacts on crops and pest species. Negative ant effects are generally associated with phenomena such as hemipteran tending which may lead to crop damage by insects in that order [23–26] or suppression of beneficial arthropods predating on hemipterans [27]. Clarification of the mechanisms behind the diverging effects of ants in different tree cropping systems has been somewhat neglected by recent works on ant ecology and behavior. No clear description exists but several characteristics can be indexed as potential reasons of the two diverging effects of ants in tree cropping systems.

This review firstly: (i) shows the agro-ecosystem services provided by ants in tree cropping agro-ecosystems in general; (ii) summarizes existing knowledge relative to the potential of ants as biological control agents; and (iii) depicts their integration and potential impact in agroecosystem insect communities. The genus *Oecophylla* is focused upon here. Secondly, it points out the potential reasons for divergence between positive and negative ant effects in tree cropping systems.

2. Services of Ants in Agro-Ecosystem Functioning

2.1. Pollinators

The flowers of insect-pollinated plants may be visited by a variety of insects whose ability to pollinate flowers varies considerably in terms of both quality and quantity [28,29]. Some groups of insects, such as ants, have been traditionally considered as inefficient pollinators, even though a few species are frequent visitors to flowers [3]. The reasons why ants are considered to be inefficient pollinators are their relatively small size compared to other pollinating insects, their commonly smooth integument, their regular cleaning of their bodies, or their antibiotic secretions (against pathogens), for which the coevolution with pollen is often incompatible [30]. The structure of certain flowers has been interpreted as an adaptation to prevent ants from visiting [31]. Another reported reason is their negligible effect on pollen flows, as it takes them, as crawling insects, a long time to move from one plant to another when compared to flying insects. The pollinating ability of ant species is considered to be low, but that assessment is relative to the existence of other much more efficient and skilled pollinators such as bees, butterflies and wasps. Nevertheless, the patrols carried out by ants on flowers gives them a status of not insubstantial accidental pollinators [32]. Philpott et al. [33] did not find any difference in the number and weight of coffee berries between trees pollinated by flying insects (bees, wasps, butterflies, etc.) or by ants. A recent study by De Vega and Herrera [34] revealed some chemical changes in the sugars of floral nectars after their contact with yeasts transported by ants. Depending on the quantity of yeast deposited, the flowers contained more fructose, more glucose and less sucrose, and registered a slight rise in temperature compared to flowers not visited by ants. This phenomenon would appear to reduce the chemical control of the plant over flower components. The ability of such flowers to be pollinated is often modified as the rise in temperature generated (around 5–6 °C) and the new nectar sugars produced would seem to attract many more pollinators such as bees [35]. However,

the interactions between yeasts transported by ants, flowers and pollinators need further investigation to gain a clearer understanding of all the ecological consequences associated with these processes.

2.2. Bioturbation Agents or "Ecosystem Engineers"

The structure of the soil in ecosystems can be affected by part of the animal biotic component, notably the soil fauna. Among the organisms of the soil fauna with a soil structuring role, earthworms, termites and ants are the most noteworthy regarding the quantity of soil they displace and the biogenic structures of organic/mineral aggregates they create (worm casts, galleries, domes, etc.) [4,5]. After earthworms, ants are the component of the soil fauna that displaces the most soil [36]. The galleries mined by ants when building nests help to aerate the soil. Some of these types of soil may be derived from relatively deep horizons and are often less rich in organic matter than some of the aggregates made by earthworms and termites [36]. Ants play a not insubstantial role in organic matter dynamics, speeding up its mineralization and the physical properties of the soil, especially its porosity, which influences water infiltration and circulation and reduces the potential risks of erosion [5,37]. Ants therefore improve the mineral quality of soil through these effects, notably through the dissolving of mineral elements such as nitrogen, phosphorus or potassium [9,38–41] and improve the availability of resources (water, sediments, nutrients, etc.) for other organisms such as microorganisms or plants [9,42,43]. These conclusions highlight the importance of ant activity in ecosystems and particularly in agricultural landscapes in which production sustainability involves the stability of ecological processes linked to soil quality.

2.3. Agents Helping to Conserve Animal and Plant Biodiversity in Ecosystems

As prey, ants are an important link in the food chains of ecosystems. Their main predators are other insects, of the families Calliphoridae, Carabidae, Chalcididae, Eucharitidae, Formicidae, Lepidoptera, Myrmeleontidae, Phoridae, Reduviidae, Rhagionidae, Staphylinidae, etc. [44], as well as arachnids; vertebrates such as toads, lizards, snakes and birds [45,46]; and even some mammals [47]. For example, in desert regions, ants are a major part of the diet of many reptiles [48,49], birds [50] or mammals [51] and make a positive contribution to maintaining the trophic network and biodiversity in such ecosystems.

Ants play an important role in disseminating seeds, to such a point that it is estimated that this phenomenon is of benefit to more than three thousand plant species, mostly in Africa and Australia [1]. Ants also play a positive role in digging seeds into the ground in synergy with the soil mellowing. Through their seed dissemination ability, they help to reduce competition between plants for space [52].

2.4. Bioindicator Agents

Oliver and Beattie [53] suggested that a good taxonomic group must satisfy four main criteria to bear the term of good bioindicator: (1) be easily sampled; (2) represent a sufficiently diversified group or with high biological importance; (3) have relationships with other taxonomic groups; and (4) be sensitive to environmental changes. Ants constitute an ideal candidate bioindicator group due to their great diversity, their large presence in almost all habitats, and the relative ease with which they can be collected [6]. Ants offer other advantages due to the relative stability of their movements compared to other insects, their ecological importance as predators, preys, detritivores, mutualists, and herbivores. Ants have been used for several years as bioindicators for resilience assessment in ancient mine sites in Australia [6,54] and in other parts of the world [55–58], for soil management and ecosystem assessment [59,60]. More specifically, their role in agricultural environments is leading them to be recognized as a useful tool to assess the impacts of management practices in farmlands [61–63]. Their use as diagnostic tool in orchards is a key element for orchard functioning since it is relatively straightforward. To confirm the hypothesis that orchard design and management practices affect ant community composition in Senegalese mango-based ecosystems, Diamé et al. [8] have shown that *Monomorium salomonis* was closely associated with high irrigation, fertilization and pesticide use,

whereas *Paltothyreus tarsatus* was associated with greater tree richness, high local ground coverage by the tree canopy, more leaf litter and great variation in the local tree planting density.

2.5. Ants: Natural Enemies and Biological Control Agents

2.5.1. Protective Activity of Ants in Relation to Plants: Generalities

Ants have developed strong associations with different organisms in their environment, and notably mutualistic interaction relationships with some plants [64,65]. Each partner in those relationships benefits from the existence of the other: ants protect plants from herbivorous insects (leaf-eating, fruit-eating, and xylophagy) and, in return, the plant provides the ants with shelter, food resources or breeding sites [66–69]. The protective role of ants is based on predation, on a repellent phenomenon, or on a phenomenon that limits the development of plant pathogenic microorganisms. The existence of certain chemical compounds carried by ants limits the development of fungi and bacteria that are plant pathogens [70]. The underlying mechanisms in this phenomenon are based on strategies used by ants through compound secretions. For instance, ants secrete antibiotics from metapleural glands [71,72]. Although they possess various means of secreting several sorts of compounds (39 different glands described so far for ants), the majority have clear functions related to the social organization of the colony [73], the production of alarm pheromones for colony defense or as compounds to maintain group identity via kin recognition [74,75]. The manner of which ants use their metapleural gland antibiotic secretions is unclear [72], however, because the mechanisms for controlling microbial diseases in cropping systems are poorly studied.

Direct predation of insects by ants depends on the type of insect, its size, its density within its environment, along with the behavior of the species of predatory ant [76]. The genus *Oecophylla* is generalist and highly aggressive, with species that manage to capture insects in their hunting territories (primary and secondary territories). On an ecosystem scale, the efficiency of predation by natural enemies also depends on the degree of complexity in the interactions between natural enemies [77,78]. In a farming environment, it is the colonization of habitats by species of dominant ants organized in the form of an "ant mosaic" (i.e., distribution of dominant species in patches, so that the territories do not overlap) [78–81] that provides the most effective control of herbivorous insects, due to the search for animal prey or honeydew as the catalyst [82]. This has particularly been seen in the species *O. longinoda* [10], *Tetramorium aculeatum* (Mayr), *Crematogaster* spp. [83] and *Anonychomyrma gilberti* (Forel) [82]. The predatory activity of ants leading to a reduction in herbivorous insect pressure (in the broad sense) is based on two main mechanisms: cooperative hunting which is considered to be the most elaborate mechanism, and so-called "stochastic" solitary hunting [84]. The predatory action of ants occurs as much in tree canopies [85–87] as it does in or on soil [88,89].

Repellence is a known phenomenon in ants to ward off insects, and it may be linked either to a chemical signal [90,91] or a visual signal [92]. Pheromone-based chemical communication occurs very frequently among ants. It may also serve as a warning signal to prey [93]. The mere presence of pheromones emitted by ants may therefore be enough to repel intruders. These chemical substances are secreted from endocrine glands located either in the insect's head, legs, or abdomen [94].

2.5.2. The Genus *Oecophylla*: An Example of an Effective Biological Control Agent in Horticulture

(1)   Ecology of the genus *Oecophylla*

The genus *Oecophylla* contains at least two species: *O. smaragdina* and *O. longinoda*. The two species have a similar ecology but *O. smaragdina* are specific to the tropical regions of Australia and Southeast Asia [95,96], while *O. longinoda* is restricted to sub-Saharan Africa [97,98] (Table 1). Both species are arboreal, building nests by weaving leaves in the canopy and displaying territorial dominance over other ant species [73,99]. The number of individuals per colony depends on biotic environmental factors such as the availability of resources (habitats, food resources, etc.) and the level of disruption to their habitats, but also on abiotic factors such as temperature and relative humidity. The size of

O. smaragdina nests in Southeast Asia varies from around 4000 to 6000 individuals and the whole polydomous colony might amount to 500,000 workers distributed among around a hundred nests scattered over fifteen or so trees [100]. In West Africa, the average nest and colony sizes are smaller and depend on the type of crop and the climate context. An orchard usually harbors several *Oecophylla* ant colonies with different colonies never co-existing on the same tree.

Table 1. African countries where the presence of *Oecophylla longinoda* ants has been reported [100,101].

Geographical Location	Country
West Africa	Benin, Burkina Faso, Gambia, Ghana, Guinea Bissau, Guinea Conakry, Ivory Coast, Liberia, Mali, Nigeria, Senegal, Sierra Leone, Togo
East Africa	Burundi, Kenya, Rwanda, Tanzania, Uganda
Central Africa	Cameroon, Central African Republic, Democratic Republic of Congo, Equatorial Guinea
Southern Africa	Madagascar, Mozambique, South Africa, Zambia

The genus *Oecophylla* is remarkable in its aggressiveness towards other insects and intruders from outside the colony. This behavioral trait helps to make it one of the most efficient ant genera for biological control. Their potential as biological control agents against a wide range of herbivorous insects is considerable in agriculture [17,102]. *O. smaragdina* and *O. longinoda*, respectively, control over 50 and 15 pest species belonging to 18 families, in eight horticultural crops [92]. *Citrus*, mango and cashew are the fruit trees that are most frequently home to these *Oecophylla* weaver ants. The genus plays a key role in integrated pest management (IPM) programmes against fruit crop pests in Australia [92,103]. The presence of *O. longinoda* in African orchards offers the possibility of developing IPM programs against various fruit tree pests, especially against fruit flies (Tephritidae), a pest of economic importance in mango orchards [8].

(2)   Importance and effectiveness of *O. smaragdina* and *O. longinoda* as biological control agents in orchards and plantations

-    *O. smaragdina* in tropical Asia and Australia

The tradition of using ants as biological control agents against crop pests is the oldest known example of biological control. The Chinese were the first to promote the control of *Citrus* pests by disseminating *O. smaragdina* nests in their orchards over 2000 years ago [16]. *O. smaragdina* are used in the orchards of the Mekong delta in Vietnam to control the leaf miner *Phyllocnistis citrella* Stainton, the red mite *Panonychus citri* (McGregor), aphids *Toxoptera aurantii* (Boyer de Fonscolombe) and *T. citricidus* (Kirkaldy), as well as a wide range of other insects harmful to citrus [16], and have helped to reduce insecticide applications by half in that region [104]. Using ants for biological control in citrus orchards in Asia and mango orchards in Australia is a well developed activity. Moreover, some studies have focused on seeking conditions that are conducive to *O. smaragdina* development in orchards [105,106].

-    *O. longinoda* in sub-Saharan Africa

In sub-Saharan Africa, research on the effectiveness of *O. longinoda* against insect pests in *Citrus* plantations is more recent, and using ants for biological control in orchards has yet to be widely developed. In Ghana, some testing of *O. longinoda* effectiveness against damage caused by fruit flies in citrus showed that the presence of *O. longinoda* in orchards could keep damage down to levels of between 6% and 10% [13]. The species *O. longinoda* is abundant in mango orchards in Benin [107] and its protective role against fruit flies has been demonstrated in mango plantations [108–110] where losses can fall by 24% when the ants are present. On farms, although some farmers have reported the merits of *O. longinoda* presence in their orchards [111], the beneficial aspect of this species in orchards

remains largely unknown to many producers. Nonetheless, they have been made aware of this over the last few years to encourage them to foster the presence of the species in orchards and its use as an alternative to pesticides [14,112]. The biological control provided by African weaver ants is not limited to mango pests (Table 2). The damage caused in cocoa plantations by pests such as *Salbergella singularis* (Hagl.), *Distantella theobroma* (Distant) and *Helopeltis* spp. can be reduced by 60% [113]. In cashew plantations, the damage caused by *Helopeltis schoutedeni* Reuter, *Pseudotheraptus devastans* (Distant), *Anoplocnemis curvipes* Fabricius, *Helopeltis anacardii* Miller and *Pseudotheraptus wayi* (Brown) on flower panicles or new leaf shoots is limited to around 6% if *O. longinoda* is present in the trees [15]. In coconut plantations *P. devastans* and *P. wayi* are also controlled by *O. longinoda*, improving productivity by an extra 2.7 to 4.1 nuts per palm on average [114].

Table 2. Examples of biological control by *Oecophylla* sp. against crop insect pests.

Biological Control Agent	Horticultural Crop	Pest(s) Controlled	Country or Area	References
Oecophylla smaragdina	*Mangifera indica*	**Curculionidae**: *Sternochetus mangiferae*	Australia	[115]
Oecophylla smaragdina	*Citrus maxima, Citrus sinensis, Mangifera indica*	**Cicadellidae**: *Idioscopus clypealis*	Thailand	[116]
Oecophylla smaragdina		**Thripidae**: *Selenothrips rubrocinctus*	Australia	[9]
Oecophylla smaragdina	*Litchi sinensis*	**Tessaratomidae**: *Tesseratoma papillosa*	China	[117]
Oecophylla smaragdina	*Citrus*	**Pentatomidae**: *Rhynchocoris humeralis*; **Aphididae**: *Toxoptera aurantii, Toxoptera citricidus*; **Gracillaridae**: *Phyllocnistis citrella*; **Curculionidae**: *Hypomeces squamosus*	South Est Asia	[117]
Oecophylla longinoda	*Mangifera indica*	**Tephritidae**: *Bactrocera invadens, Ceratitis cosyra*	Benin	[110,111,117]
Oecophylla longinoda	*Mangifera indica*	**Tephritidae**: *Bactrocera invadens, Ceratitis* spp.	Benin	[109]
Oecophylla longinoda	*Theobroma cacao*	**Miridae**: *Salbergella singularis, Distantella theobroma, Helopeltis* spp.	Ghana	[114]
Oecophylla longinoda	*Anacardium occidentale*	**Miridae**: *Helopeltis schoutedeni*; **Coreidae**: *Pseudotheraptus devastans, Anoplocnemis curvipes*	Ghana	[15]
Oecophylla longinoda	*Anacardium occidentale*	**Miridae**: *Helopeltis schoutedeni*; **Coreidae**: *Pseudotheraptus devastans, Anoplocnemis curvipes*	Benin	[118]
Oecophylla longinoda	*Anacardium occidentale*	**Miridae**: *Helopeltis anacardii, H. schoutedeni*; **Coreidae**: *Pseudotheraptus wayi*	Tanzania	[119]
Oecophylla longinoda	*Citrus* spp.	**Tephritidae**: *Ceratitis ditissima*	Ghana	[13]
Oecophylla longinoda	*Cocos nucifera*	**Coreidae**: *Pseudotheraptus devastans*	Ivory Coast, Tanzania	[114,120]

- Mechanisms used by *O. longinoda* in biological pest control

The mechanisms whereby *O. longinoda* biologically controls insect pests takes two forms: direct and indirect. In the direct form, *O. longinoda* predates on insect pests or neutralizes pathogens with antibiotic compounds. In the indirect form, a repellent phenomenon is involved. Predation of insect pests takes place on trees housing nests, and in the "secondary" territories usually located below the trees on the ground [102]. This ability to eliminate any intruders in their territory makes *O. longinoda* interesting to many researchers. The ant species has developed some efficient strategies for hunting in groups and capturing insects on the foliage of trees, but also on the ground, at the foot of the tree on which they nest [102,121,122]. The repellent phenomenon occurs via a chemical or visual signal that wards off pests from the territories patrolled by *O. longinoda*. Some research has shown that *O. longinoda* causes a repellent reaction against fruit flies responsible for major production losses [111,112,123]. Although the mechanisms brought into play in the repellent phenomenon exerted by *O. longinoda* have

not been widely documented, they would nonetheless seem to be linked to pheromone signals that are perceived by insect pests. Some laboratory tests showed that fruit flies greatly reduced the frequency of their visits to fruits exposed to weaver ants [109,124]. The repellent action of *O. longinoda* against highly mobile pests such as fruit flies is backed up by the hypothesis of the emission of chemical pheromones that the latter can perceive and to which they react by moving away [125] or even by a change in their egg-laying behavior, reducing the time spent laying eggs [108–110,123]. This repellent phenomenon thus appears to limit the damage caused by fruit flies on trees occupied by weaver ants.

(3)　　Problems with adoption of the genus *Oecophylla* by farmers

Two types of problems may arise with weaver ants in the eyes of researchers and farmers. These are their interactions with Coccidae mealybugs and their bites on humans.

- Interactions with Coccidae scale insects

Homoptera are often considered to be crop pests but this is not always true. The farming of scale insects by weaver ants in fruit tree plantations actually raises some questions about the protective role of weaver ants on fruit trees. After determining the main species of *Coccidae mealybugs* found on mango leaves, flushes (growing shoots) and fruits (protected by *Oecophylla*) in Benin, it appeared that: (i) most are scale insects without any negative impact on mango; and (ii) the mango flesh is never damaged by the scale insect's stylets [125]. In addition, the species of mealybugs that are mango pests, such as *Rastroccocus invadens* Williams, are never conveyed or protected by *Oecophylla* [126]. However, this could be a problem on other fruit trees so it is an issue that needs to be studied before promoting weaver ants as a biological control on a new fruit tree species, especially when the Homoptera present on the fruit species are also virus vectors. The indirect effect mealybugs may have on reduced growth/productivity by weakening the plant via sap feeding also has to be considered. According to Peng and Christian [103], an effective way of getting rid of the scale insect problem may be to use low-toxicity insecticides such as potassium or white oils that can reduce populations of these undesirable insects without having an impact on the ant populations. However, organophosphorous and pyrethroid insecticides should be avoided at all costs in orchards with weaver ants [100].

- Bites

Weaver ant bites during harvesting are often a main problem cited by farmers or workers. Different strategies are adopted by populations to reduce this nuisance [103,127]. The nuisance caused by bites can be reduced by adopting mechanical avoidance procedures (long harvesting pole, suitable clothing with rubber gloves and boots), mechanical repellence procedures (ash applied on hands and legs), chemical repellence procedures (spraying water in which cassava leaves have been soaked, and application of a saline solution or lemon juice on the exposed areas of the body), working on trees at the coolest times of day (very early in the morning) or the hottest (middle of the day), or behavioral procedures (movement with slow steps and avoiding walking on their trails). Mechanical avoidance and repellence procedures have been well adopted by farmers in West Africa who have been made aware and supervised through, for example, research and development projects (Benin, Burkina Faso, Guinea and Mali), and by farmers in Asia (Thailand, Vietnam, Malaysia, Australia and others) [127]. Nevertheless, this issue calls for some more research work to encourage the adoption of weaver ants as biological control agents in orchards, particularly as none of the practices used by farmers have been scientifically assessed to date.

(4)　　*Oecophylla* sp. in the trophic food web in agro-ecosystems

- Sustaining *Oecophylla* ants in agro-ecosystems

Using ants for biological control has gained some ground over the last 10 years in Africa, due to the intensification of damage by fruit flies since the arrival of *Bactrocera dorsalis* (Hendel) in the western part of the continent. Research and the deployment of IPM programs using *O. longinoda* ants in

Benin [110,111,123], Ghana [15] and Tanzania [119,128] are of great importance from a socio-economic viewpoint for farmers who often have very limited resources. The management of the *Oecophylla* has been well documented by Van Mele and Cuc [100] who summarized the easiest ways and practices to support their populations in orchards.

Managing a whole community of ants proves to be more difficult than just a single species, which is why many biological control programs adopt the process for just one species of ants. However, the advantage of an approach using a whole community of ants is that the complexity of the interactions found in the diversity of ants may provide greater flexibility in controlling crop pests [129].

Perfecto and Castiñeiras [129] reported that some potentially complex interactions between ant species might influence the effectiveness of biological control in plantations. According to Seguni et al. [128] the competition that might exist, for example, between the species *O. longinoda* and *Pheidole megacephala* (Fabricius) for occupation of the canopy, may reduce the effectiveness of the biological control exerted by *O. longinoda* on *Pseudoptheraptus wayi* (Brown), a coconut pest. Rapp and Salum [130] demonstrated that it is possible to reduce such competition with appropriate practices. They stipulated that keeping weeds in oil palm plantations altered competition between the two species and increased by more than twofold the number of palms colonized by *O. longinoda* in one year.

This type of management is the reverse of orchard management where humans seek to eradicate a pest using chemical pesticides, a practice that proves to be harmful as it is likely to cause: (i) the elimination of natural control agents through lethal and sub-lethal effects; (ii) an imbalance in the trophic chains; (iii) the emergence and/or resistance of new biotypes and/or new species of pests; and (iv) the selection or favoring of dominant ant groups [131]. Moreover, studies by Kenne et al. [132] showed the negative impact of applying chemical pesticides which led to dominant species being selected, such as *Myrmicaria opaciventris* Emery, *P. megacephala*, *Camponotus acvapimensis* Mayr and *Paratrechina longicornis* (Latreille) in citrus, guava and mango plantations in Cameroon. These species very often farm species of phytophagous Homoptera that are harmful to crops [132]. Avoiding such a situation again means reconsidering the importance of plant biodiversity conservation and management practices which scientists interpret as being an important functional element in orchards, whereas farmers very often only show an interest in biodiversity to optimize the use of their agricultural land, i.e., intercropping, or the services it may provide as shading or windbreaks for crops [105].

- Interactions with the other natural enemies

Ants play a key role in tropical agro-ecosystems [133,134], with some indigenous or invasive species frequently reaching large numbers and becoming ecologically dominant over other ant species [73]. Dominant ant species can reduce the species richness of natural enemies and the ecological stability of the trophic network due to their aggressive behavior, which excludes those species from their territory and their source of food [135]. Omnivorous and generalist predators such as weaver ants are rivals able to tolerate a low level or, up to a certain degree, an absence of prey, which can create asymmetric competition for the resource. Moreover, in addition to feeding off their usual prey, omnivorous predators sometimes attack their intraguild competitors, i.e., intraguild predation behavior, which strengthens their superior competitor status. This is why the question of interactions between *Oecophylla* sp. and other natural enemies of crop pests lies at the heart of our investigations.

When studying of *O. smaragdina* impact on insect biodiversity, Peng and Christian [10] showed that mango and cashew orchards with large *Oecophylla* ant populations had a similar or greater diversity of arthropods and natural enemies and similar natural enemy/insect pest ratios compared to orchards without weaver ants. However, one species of spider (*Oxyopes* sp.) was rarely caught in cashew and mango orchards with large numbers of weaver ants, suggesting that the ants were involved in the predation or repellence of *Oxyopes* sp. They then noticed that the *O. smaragdina* ants and the *Oxyopes* sp. spider had very similar ecological niches and that, consequently, the spider was being subjected to fierce competition. Another laboratory study [136] focusing on the interaction between *O. longinoda* and the parasitoid *Fopius arisanus* (Sonan) (Hymenoptera: Braconidae) demonstrated

that *F. arisanus*, a parasitoid of the fruit fly *B. dorsalis*, reached parasitism rates on *B. dorsalis* that were significantly higher on mangoes not exposed to *O. longinoda* compared to mangoes exposed to that species. In this case study on *B. dorsalis* and its natural enemies, the effectiveness of the indigenous parasitoid *F. arisanus* on *B. dorsalis* was very low [137,138]. If similar results were to be found under natural conditions (in orchards), this could become problematic in a classical biological control program context, i.e., introduction of the exotic parasitoid *F. arisanus* throughout the African continent. In West Africa, and under natural orchard conditions, however, observations carried out since 2005 in Benin have yet to identify an aggressive behavior of *O. longinoda* towards parasitoids of Tephritidae (J.-F. Vayssières, personal communication). It is also essential to note that the negative effects of intraguild interactions on biological control are usually not great enough to cancel out the benefits linked to the association of several natural enemies to control a pest [139–141].

- Interactions with pollinators

Another group with which *Oecophylla* ants might interfere negatively is pollinators. However, here again, the situation is not clear and this potentially negative effect has only been investigated recently [142–144]. As predators patrolling on all tree organs including flowers, weaver ants can be suspected of predation on pollinators. Indeed, the results obtained by Tsuij et al. [145] in a rambutan orchard (hairy lychee, *Nephelium lappaceum*) in Sumatra suggested that the presence of weaver ants significantly reduced the number of visits to flowers by flying insects, including the major pollinator *Trigona minangkabau* (Apidae: Meliponinae). On the other hand, Pierre and Idris [146] found that weaver ants did not disturb the oil palm pollinator *Elaeidobius kamerunicus* Faust (Coleoptera: Curculionidae) in Malaysia. According to Rodríguez-Girones et al. [147], although ants are not usually considered to be flower-dwelling ambush predators, this needs to be reconsidered, at least in the Tropics. They therefore propose weaver ants (*O. smaragdina*) as a new model for studying ambush predators. In their study, they found that weaver ants were present on the flowers and attacked the insects visiting the flowers of 31 of the 48 plant species studied. Such observations have not been carried out for the species *O. longinoda*, but it has nonetheless been shown that certain flowers existing on the African continent produce some substances that repel *O. longinoda* [148], which suggests that *O. longinoda* is potentially a flower-dwelling ambush predator, interfering with pollination.

However, the complexity of the interactions between species is so great that the effects which appear, at first glance, to be negative may ultimately prove to be positive. For example, *O. smaragdina* is known to be a predator of the fig tree (*Ficus* spp.) pollination wasp, but, when studying the impact of weaver ants on this mutualism between crop and pollinator in greater detail, Schatz et al. [149] suggested that they might ultimately have a positive effect on pollination as they had a dissuasive effect on parasitic wasps, which might compensate for their theoretically negative effect on pollinating wasps. In fact, pollinating wasps seem to benefit from the predation of weaver ants on parasitic wasps. Another example is the study by Gonzálvez et al. [150] showing that the presence of weaver ants on *Melastoma malabathricum* Linnaeus (Melastomataceae) was associated with an increase in flower reproduction, as they tended to hunt the least effective pollinators, thereby favoring the presence of the most efficient.

For fruit agro-ecosystems, it is a matter of knowing whether a satisfactory compromise can be found between the benefits of the presence of weaver ants (predation of pests) and their negative effect on pollination. The fact is that it is very difficult to predict: (i) the effect of weaver ants on fruit tree pollinators; and (ii) the impact of the drop in pollinator access to flowers on tree yields. Indeed, very few data are available on fruit tree pollinators in the Tropics. Nevertheless, mango [151], cashew [152] and *Citrus* [153] mainly seem to be dependent on pollination by insects. However, very few studies have been undertaken on the African continent [154]. Consequently, the impact of *O. longinoda* ants on fruit tree pollination in African orchards, when they are used as a biological control agent, calls for further studies, as is currently the case in Benin [118].

3. Potential Reasons for Divergences between Positive and Negative Ant Effects in Cropping Systems

Ant research rarely compares the potential reasons that certain ant species have negative effects while others have only positive ones in cropping systems but a comparison between these two effects has shown that different elements are determinant in ant ecology and behavior. Although there is a lack of accurate work concerning this issue, a comparison between these two effects has shown that different elements are determinant in ant ecology and behavior. These elements are relative to their bio-ecology. For instance, since temperate regions offer limited resources for ants, due to a lower plant diversity compared to tropical regions, tree cropping systems represent a target for ants with their associated trophobionts to complete their diet, or to easier predation (L. Diamé. personal communication). Tropical cropping systems offer more plant diversity, more habitat heterogeneity and variety of food webs. Thus, they are more conducive to ants seeking food and habitats. Consequently, the ants are more likely to become tree crop pests. However, a deep and clear analysis for exact explanations has proven difficult so far because there is a lack of studies to confirm these suppositions.

Intraguild competition in ant communities is a key element to take into account for describing ant characteristics. When considering competition for space or habitat occupation in ant communities, the result can either be positive or negative to tree crops [127]. Habitat simplification, or monoculture, leading to a low plant diversity generally creates conditions which select only dominant ants [8] with possible negative impacts from hemipteran-tending depending on the ant species involved [132,155].

Understanding ant characteristics involves dealing with their bio-ecology. New agricultural conditions such as biogeographical area, climate change, and altered bio-ecology of species are among several potential elements determining their behavior. Their relationships towards tree crops seem to be dependent on situations offering colony survival and sustainability conditions in any habitats or climates. The only manner to clarify these suppositions is to undertake relevant studies.

4. Discussion and Conclusions

Agro-ecological management of an orchard appears to be an approach that incorporates different functional elements of the agro-ecosystem with a view to increasing its self-regulation capacity. This calls for greater consideration of the biodiversity of arthropods living in the orchard and a clearer understanding of the role played by each species there, along with their interactions. Within an agro-ecosystem, the animal component is known to be a decisive element for plant production through flower pollination, as well as for biological control by natural enemies. Herbivory is also an important component of animal–plant interactions with either positive or negative effects. The very real contribution of ants to nutrient recycling, decomposition of organic matter, soil structuring, and limiting disease development on plants, is an additional asset supporting their use as biological control agents in agro-ecosystems. IPM programs seem to provide a relevant tool that is in keeping with an agro-ecological approach, insofar as it is the trophic interactions between biotic components in the environment that are favored, to the detriment of phytosanitary intervention based on highly toxic chemicals. A combination of biological control by ants and IPM is suggested for controlling a variety of pests in cocoa, mango, cashew or banana plantations [18]. The effective adoption of this approach remains relatively low in the majority of African fruit agro-ecosystems. Promoting ant populations in tree cropping systems is possible. The use of *Oecophylla* either by introduction or through conservation of habitat in regions where it is endemic and trophic food web is an example of its successful use in biological control programs in orchards [100].

The interactions between ants and the Homoptera they farm, the formic acid secretions which give fruits a less attractive appearance, and the physical nuisance caused by ants during fruit harvesting are problems that are very often raised as obstacles to adopting ants as biological control agents [18].

Certain criteria need to be taken into account when choosing a species of ant to be adopted/ encouraged as a biological control agent in IPM programs. First, it is important to identify the ant fauna already present in the agro-ecosystem. Hölldobler and Wilson [73] highlighted that the taxon

is not exhaustively known, and Ward [156] even suggested that there may be twice as many species as currently identified. Taxonomic efforts, however, have intensified in recent years although much more is needed. The next stage is to study the ecology of all the species present to select the one that may be most efficient. Indeed, the phenology of a species, its hunting behavior, as well as its relations with other natural enemies, with Homoptera and Hemiptera, or with humans, are all factors likely to influence the skillfulness and ability of the chosen ant species in controlling the target pest [18].

Although the biological control agent role is the most visible function of ants, the information gathered in this review has provided an exhaustive presentation of the other multiple roles played by ants in agro-ecosystems. The negative aspects put forward regarding ants in agro-ecosystems seem to be clearly outweighed by their positive effects. As far as the interactions between weaver ants and fruit crop pollinators are concerned, it would be worth taking a closer look at the insect pollination requirements of these plants and up to what point these pollinators can be affected by ants without impacting crops. The role of ants as soil structuring agents, pollinators or agents contributing to biodiversity conservation are still not taken into account enough in studies of agro-ecosystem functioning in West Africa. There is thus a great need for research to determine more effectively the contribution made by certain ant species in soil processes, their interactions with elements of the soil fauna and their relationships with all the trophic chains, which are very important parameters in the functioning of tropical agro-ecosystems.

However, crucial questions relative to ant effects in cropping systems are still in suspense. Continued ant bio-ecological research is necessary in respect to its potential value in improving tree cropping production conditions. Among several potential future directions in ant bio-ecology, a clarification of the divergences between positive and negative effects on cropping systems should represent a real advance for ant ecology knowledge.

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