The use of weaver ants in the management of fruit flies in Africa

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Abstract

Generalist predators such as the weaver ant, *Oecophylla longinoda* (Latreille), play an important role as biological control agents in West African orchards and, by extension, also in forest and savanna ecosystems within sub-Saharan Africa. These weaver ants are one of the most effective and efficient predators of arthropods in perennial tropical tree crops; their presence also acts as a deterrent to insect herbivores, particularly tephritid female fruit flies, due to the semiochemicals they produce. Emerging African markets for organic and sustainably-managed fruits and nuts have encouraged an interest in the use of weaver ants. Protection of tropical forests and savannas is ecologically and environmentally crucial and also essential for the protection of *O. longinoda*.

Keywords: *Oecophylla longinoda*, Tephritidae, trophic interactions, ant cues, conservation biological control.

1. Introduction

Generalist predators, such as the weaver ant, *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae: Formicinae), play an important role in orchard, forest and savanna ecosystems in sub-Saharan Africa (Leston 1973). Weaver ants are highly effective and efficient in controlling arthropod pests in perennial crops due to their tireless predatory activities (Dejean 1991). The presence of weaver ants also deters the activity of insect herbivores such as fruit flies (Diptera: Tephritidae) who recognize and avoid semiochemicals produced by the ants (Adandonon et al. 2009). Under some conditions fruit fly populations can be controlled by biological control agents such as parasitoids and generalist predators like *Oecophylla* species (Van Mele and Cuc 1999).

To determine the conditions necessary to enhance pest regulation by natural enemies, it is necessary to better understand the exact nature of their interactions across all trophic levels in the food web (Dejean 2007). Interactions affecting the abundance of organisms may be direct or indirect and can have cascading effects across several trophic levels (Table 1) in the ecosystem before they influence fruit productivity and quality (Vayssières 2012). A detailed understanding of the ecology and behaviour of natural enemies is, therefore, essential if we are to encourage their activity against fruit flies within integrated management strategies (Quilici and Rousse 2012).

2. Fruit flies in sub-Saharan Africa

African fruit producers throughout sub-Saharan Africa, and particularly in certain regions and countries, are confronted with a number of closely connected problems: (a) severe deterioration of fruit quality due to fruit flies (White and Elson-Harris 1992; De Meyer et al. 2007); (b) inadequate post-harvest fruit fly control methods (Van Melle and Buschmann 2013); (c) invasive plant diseases such as *Xanthomonas citri* pv. *mangiferaeindicae* (Patel et al.) comb. nov., which causes mango bacterial canker across Ghana and Benin (Pruvost et al. 2011a, b; Zombré et al. 2015) and *Phaeoramularia angolensis* (De Carv. & Mendes) P.M. Kirk which causes citrus fruit and leaf spot in West Africa (Vayssières 1995); (d) over-production in national markets leading to wastage and low prices (Vayssières et al. 2009a); (e) inadequate selection of appropriate mango (*Mangifera indica* L.) varieties (Vayssières et al. 2008); and (f) underdevelopment and/or under-utilisation of export markets (Van Melle and Buschmann 2013).

In sub-Saharan Africa, many fruit fly species attack agricultural crops. Amongst them, six are considered of the greatest economic importance: the mango fruit fly, *Ceratitis cosyra* (Walker); the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann); the Natal fruit fly, *Ceratitis rosa* Karsch; and three exotic invasive species, the peach fruit fly, *Bactrocera zonata* (Saunders) that has been present in Sudan for several years (Salah et al. 2012); the melon fruit fly, *Zeugodacus cucurbitae* (Coquillett) (De Meyer et al. 2015); and *Bactrocera invadens* Drew Tsuruta & White. The latter has recently been placed in synonymy with the oriental fruit fly *Bactrocera dorsalis* (Hendel) (Schutze et al. 2014a, b).

Bactrocera dorsalis, originating from South-East Asia, was found for the first time in Africa in Kenya in 2003 (Lux et al. 2003) and then in Tanzania (Mwatawala et al. 2004). This invasive species was subsequently reported in Sudan (Luckman 2004), Senegal (Vayssières 2004), then in Côte d' Ivoire (Hala et al. 2006), Cameroon (Ndzana Abanda et al. 2008), Nigeria (Umeh et al. 2008), and subsequently in other African countries (Vayssières et al. 2010a). *Bactrocera dorsalis* causes extensive economic losses to horticultural crops throughout sub-Saharan Africa and is especially harmful to the mango value chain in East and West Africa (Ekesi et al. 2006; Vayssières et al. 2009a), increasing the already considerable damage caused by native fruit flies. With its high reproductive rate (Ekesi et al. 2006; Salum et al. 2013; Gomina et al. 2014), a large host plant range (De Meyer et al. 2007; Rwomushana et al. 2008; Mwatawala et al. 2009a; Goergen et al. 2011) and high mobility (Vayssières et al. 2009b), this species is a major pest of economic significance.

In Benin several fruit value chains of commercial interest are severely jeopardized by *B. dorsalis*, such as mango (Vayssières et al. 2009a), citrus (Vayssières et al. 2010b) and guava (Vayssières et al. 2010c). According to Ekesi et al. (2009) and Salum et al. (2013) exploitative competition through larval scrambling for resources and interference competition accompanied by the aggressive adult behaviour of *B. dorsalis* compared with native species, are important displacement mechanisms. As a result, *B. dorsalis* has displaced *C. cosyra* in mango agro-ecosystems and out-competed *C. capitata* in citrus plantations (Vayssières et al. 2010b). *Bactrocera dorsalis* has changed the landscape of pest fruit flies in Africa.

Studies on fruit fly control have been conducted in: Southern Africa (Labuschagne et al. 1996; De Meyer 2001, 2005; White 2006; Correia et al. 2008; Grové et al. 2009; De Villiers et al. 2013; José and Santos 2013; Hill and Terblanche 2014; Manrakhan et al. 2015);

in East Africa (De Meyer 2001, 2005; Lux et al. 2003; Ekesi et al. 2006, 2009; Mwatawala et al. 2006a, b, 2009a, b; Copeland et al. 2006; White 2006; Rwomushana et al. 2009; Geurts et al. 2012, 2014; Salum et al. 2013); in central Africa (De Meyer 2001, 2005; Ndzana Abanda et al. 2008; Ngamo et al. 2010; Virgilio et al. 2011; Mayamba et al. 2014); and in West Africa (Vayssières and Kalabane 2000; Vayssières et al. 2004, 2005, 2008, 2009a, b, 2010a, b, c, 2011a, 2012, 2014, 2015a; De Meyer 2001, 2005; Hala et al. 2006; Ndiaye et al. 2008, 2012, 2015; Umeh et al. 2008; Amevoin et al. 2009; Appiah et al. 2009; N'Dépo et al. 2009, 2010, 2013; Ouedraogo 2011; Ouedraogo et al. 2011; Zakari et al. 2012; Gomina et al. 2014).

3. Importance of natural enemies, particularly predators, in controlling fruit flies

Biological control is the use, by introduction, augmentation and/or conservation of beneficial organisms to control harmful organisms. In the case of fruit fly pests, the main biological control agents known to date are parasitoid wasps (Hymenoptera: Braconidae, Eulophidae, Pteromalidae), ant predators (Hymenoptera: Formicidae) and a fungus called *Metarhizium anisopliae sensu lato* (Metschn.) Sorokin (Ekesi et al. 2003).

Releases of parasitoids, mainly Braconidae, have shown promise for the area-wide management of tephritid pests, either as part of classical biological control programmes against exotic species, or augmentation programmes against native species (Wharton 1989; Sivinski et al. 1996). In several West African countries, we found that immature stages of fruit flies were parasitized by a wide range of parasitoid species. Only a few of them are appropriate for biological control (Sivinski et al. 1996; Quilici and Rousse 2012). To date, nearly all the actual or potential biological control agents are egg or larval parasitoids, frequently from the family Braconidae, subfamily Opiinae. The Opiinae are the most abundant and species-rich group of tephritid parasitoids and are frequently used in biological control or as part of integrated pest management programmes. The most common hosts are known for almost half of the currently recognized parasitoid species (Wharton 1997; Rugman-Jones et al. 2009) and they are all solitary, koinobiont endoparasitoids of Tephritidae, developing inside immature flies and killing them in the process. In response to the success achieved in Hawaii and elsewhere in the biological control of several *Bactrocera* species of economical importance (Vargas et al. 1993, 2007), the braconid parasitoid *Fopius arisanus* (Sonan) has been introduced into several African countries including Benin, Kenya, Senegal and Togo (Goergen, personal communication). While it appears that repeated releases have resulted in parasitoid establishment in these countries, their overall impact on fruit fly populations under afrotropical climatic conditions remains to be assessed. An initial small scale study in Senegal to evaluate impacts on fruit fly populations has shown that mangoes in the control orchard were 5–6 times more heavily infested with fruit flies than mangoes in the orchards where *F. arisanus* was released (Ndiaye et al. 2015).

The braconid genus *Psyttalia* also bears some potential but more fundamental studies are required (Billah et al. 2008). Other families of tephritid parasitoids, such as the Eulophidae (koinobionts) and the Pteromalidae (idiobionts), are less frequently used in biological control of tephritid pests. Use of the fungus *M. anisopliae* is another effective way of fruit fly control as developed and successfully tested by *icipe* in East Africa (Ekesi et al. 2005, 2007, 2011).

Species of weaver ant in the genus *Oecophylla* Smith, 1860 (Hymenoptera Formicidae) are a key element within conservation biological control approaches targeted at tephritids in several regions (Peng and Christian 2006; Van Mele et al. 2007). In conservation approaches, the biological control agents concerned are not introduced or augmented but naturally occurring individuals are encouraged through cultural practices (Vanderplank 1960). The Asian weaver ant, *Oecophylla smaragdina* (Fabricius), has provided protection of citrus trees against tephritids in Southern China since the fourth century AD (Huang and Yang 1987; Barzmann et al. 1996). More recent reports have demonstrated that *O. smaragdina* provided protection against fruit flies in Asian and Australian cashew (*Anacardium occidentale* L.) and mango orchards (Peng et al. 1995; Van Mele and Cuc 2000; Peng and Christian 2006). The weaver ant, *Oecophylla longinoda* (Latreille), a close relative of *O. smaragdina*, is distributed across sub-saharan Africa but its potential for control of tephritids has received less attention until recently. Since 2005 exploratory studies on this species have been ongoing in Benin, West Africa.

3.1. Distribution of the genus *Oecophylla*

To date the genus *Oecophylla* has been recorded throughout forested regions of the Old World tropics (Figure 1). There are only two *Oecophylla* species globally, both of which are exclusively arboreal: the African species *O. longinoda* (Figure 2) and the Asian species *O.*

smaragdina (Figure 3a). The African species is widespread throughout sub-Saharan Africa between the sixteen-degrees-north latitude and the twenty-degrees-south latitude (Lokkers 1986). However, these general data require fine-tuning for each sub-Saharan country. The Asian species extends from Southern Asia, including India, to northern tropical Australia including many tropical western Pacific islands (Cole and Jones 1948). Both species are similar in their ecological and morphological traits with powerful mandibles (Figure 3b). *Oecophylla smaragdina* can be distinguished by its very slender petiole, its very prominent stigmata, and its ventral surface which is nearly straight or very feebly convex in profile; in contrast, *O. longinoda* has a stouter and higher petiole (Figure 2), with the stigmata not prominent from above, and the ventral surface strongly convex in profile (Wheeler 1922).

The critical parameters that positively affect the distribution of *Oecophylla* species are (i) perennial vegetation, (b) temperatures above 18°C, (c) high annual rainfall (above 500mm) (Lokkers 1990), (d) low altitude (in relation to the temperature threshold), but also (e) conservation measures that enhance densities in plantations. Even though these critical thresholds, especially rainfall and temperature, can help to explain delimitation of *O. longinoda* in the African Sudano-Sahelian zone, further field work is necessary to determine the exact limits for the presence of the weaver ant in this zone. The distribution of *O. longinoda* remains unclear with regard to its northern limit within the south-Sahelian zone, and it has been suggested that climate change may impact on this (Vayssières 2012). Under favourable conditions the ant can survive in the Sahelian zone, as was observed in mango plantations at the fruit station of Kaedi (Mauritania 16.1353N - 13.5826E) from 1987 to 1991 (Vayssières et al. 1991); however, it seems that *O. longinoda* is currently no longer present in this location.

3.2. Key traits of the African weaver ant, *O. longinoda*

The genus *Oecophylla* belongs to the sub-family Formicinae, an ant taxon lacking a functional sting. The painful 'sting' reported by fruit growers is actually the ant's bite, which it inflicts with its powerful mandibles. *Oecophylla longinoda* is a large ant reaching up to 9mm in length; the species is characterized by populous colonies and the ability to build large and polydomous nests with a highly developed intra- and interspecific territoriality (Crozier et al. 2009) that allows populations to be distributed in a mosaic pattern in tree canopies (Majer 1972; Dejean et al. 1994; Blüthgen and Stork 2007).

Oecophylla longinoda is endemic to sub-Saharan Africa and frequently found in forested wild vegetation and unsprayed orchards of: mango, *Mangifera indica* L. (Figure 4a); *Citrus* species; (Figure 4b); cashew, *Anacardium occidentale* L. (Figure 4c); guava, *Psidium guajava* L. (Figure 4d); custard apple, *Annona muricata* L.; cocoa, *Theobroma cacao* L.; coconut, *Cocos nucifera* L.; coffee, *Coffea* x *arabusta* Capot & Aké Assi; and oil palm, *Elaeis guineensis* Jacq. amongst others. Many tropical trees, shrubs (Figure 5a, b) and lianas can host this common arboreal ant species. Detailed accounts of the ecology of *O. longinoda* (Wheeler 1910; Ledoux 1950; Way 1954a), its behaviour (Wheeler 1910; Ledoux 1950; Chauvin 1952; Way 1954b; Sudd 1963; Wilson 1971; Hölldobler and Wilson 1977), and its role in plant protection (Way 1953; Vanderplank 1960; Sudd 1963; Dejean 1991; Varela Barros 1992; Peng et al. 1995; Offenberg 2015 amongst others) are available.

Each *O. longinoda* colony maintains its territory and coordinates its activities using a highly developed chemical communication system in combination with visual and tactile cues (Hölldobler and Wilson, 1978). They secrete various pheromones from their heads but also from sternal and rectal glands (Hölldobler and Wilson 1990). With their large colonies and their ability to build nests almost anywhere (with the exception of many urbanized areas), *O. longinoda* populations are able to closely control their environment. In African savannahs and forests, the construction of numerous communal silk nests by each colony has probably facilitated the success of these arboreal ants (Hölldobler and Wilson 1990). Different life stages and forms can be distinguished in a colony and include the queen (Figure 6a), males, small and large workers (Figure 6b), pupae and larvae. Way (1954a) observed one colony of *O. longinoda* inhabiting 151 nests, scattered throughout eight coconut trees and four clove trees (*Syzygium aromaticum* (L.) Merrill & Perry) covering an area of 800 m^2. He estimated that this colony contained 480,000 worker ants and 280,000 brood. Similarly, in an assessment of the abundance of *O. smaragdina* in Australian mango plantations, it was found that the biomass of colonies was up to almost 3 kg per colony and that the average number of worker ants per occupied mango tree was up to 60,000 individuals (Pinkalski et al. 2015). Such dense worker populations may afford intensive patrolling in the canopies of host trees.

3.3. Colony establishment and reproduction in *O. longinoda*

Various authors have revealed the importance of different patterns of vegetation on *O. longinoda* distribution (Leston 1973; Room 1971; Majer 1972; Way 1963). Many types of vegetation can support *O. longinoda*, and vegetation manipulation can induce changes in the ant-mosaic. *Oecophylla longinoda* requires thick vegetation, especially perennial species, usually with an interconnected canopy to provide nesting sites and foraging areas (Taylor and Adedoyin 1978). Nests of *O. longinoda* can be found in different positions, at different heights in the tree, and on many tree species; they can utilize many plants in a wide range of tropical habitats (Dejean et al. 1999). In West Africa, the nests of *O. longinoda* are commonly found in (i) fruit plantations (such as mango, citrus and cashew), (ii) wild hosts (trees, shrubs and lianas) around fruit plantations, and (iii) in dry as well as humid forests (Vayssières 2012). In Benin, *O. longinoda* nests were recorded on 34 tree species belonging to 21 families (Vayssières 2012) with new records continuously being added.

Oecophylla longinoda ants are highly organized when building their nests (Ledoux 1950; Chauvin 1952; Way 1954a; Hölldobler and Wilson 1977). In Benin leaves of some mango cultivars (e.g. Keitt) which are very long and narrow, were first pulled together edge to edge by the large workers building chains between the leaves by attaching to each other; by shortening these chains the leaves were forced together (J.-F. Vayssières, personal observation). Then the leaves were joined together with silk produced by the last larval instars (both females and males) that were held as a tool by the worker ants (Figure 7) (Hölldobler and Wilson 1977). Only the larvae of *Oecophylla* species can produce silk. In the nest, some of the walls and galleries are made entirely of silk.

Winged male and female sexual stages are produced during the rainy season, which is also when nuptial flights take place (Way 1954b; Rwegasira et al. 2015). Both haplometrotic colony founding (by a single queen) and pleometrotic colony founding (by multiple queens) have been recorded (Ledoux 1950; Vanderplank 1960). The alate (winged) queens that leave the colony during the nuptial flight become founders of new future colonies. Such new queens can be attracted to artificial nests (Figure 8) where they detach their wings, seek shelter and settle during their founding stage (Ouagoussounon et al. 2013, 2015). Queens caught in artificial nests can be used to establish new colonies for farmers. In order to favour the development of large *O. longinoda* populations, transplantation of pupae may be used to shorten the time needed to produce mature *O. longinoda* colonies in ant nurseries (Ouagoussounon et al. 2013). These methods could be used to implement biological control of fruit flies by *O. longinoda* throughout West and sub-Saharan Africa (Ouagoussounon et al. 2013).

Once established, there are many constraints that threaten the viability of *O. longinoda* populations. Its main abiotic constraint is the harsh environment, especially long and dry winds such as the harmattan (dusty trade wind in western Africa, blowing from the Sahara into the Gulf of Guinea during the dry season) combined with long drought periods with low temperatures (December-January). Other major constraints are (i) limited food supply, (ii) unsuccessful mating, (iii) the use of insecticides by farmers, and (iv) bush fires (Vayssières, 2012).

3.4. Host-plants and associated trophobionts exploited by *O. longinoda*

Oecophylla longinoda are mostly found on plants that also support heteropteran symbionts, also known as trophobionts. These trophobionts excrete sugar-rich honeydew, which the ants feed on. Since *O. longinoda* obtain rich sugar and amino acid food sources via these interactions, in return they protect the trophobionts from predators and parasitoids (Way 1963). Trophobionts are a key component in tropical foodwebs that link ants with plants. The presence of trophobionts improves the establishment of *O. longinoda* colonies first by providing the ants with sugar and secondly by serving as alternative prey (i.e. a protein source) when the predatory activities of the ants are unsuccessful. This is particularly the case during the dry season when, in the Sudan zone of Benin, *O. longinoda* also obtain nutritional ressources by harvesting seeds (Figures 9a, b) and plant debris (Figure 9c) (Vayssières et al. 2015b). There are several species of trophobiont species that *O. longinoda* colonies tend for food and they come from the families: Coccidae (Figure 10a), Pseudococcidae, Stictococcidae, Membracidae and Tettigometridae (Figure 10b) (Bluthgen et al. 2004). Across Benin, approximately 20 species of Coccoidea (Table 2) have been reported interacting mutualistically with *O. longinoda* (Vayssières 2012). In the three agroecological zones of Benin the most common species associated with *O. longinoda* on mango is the coccid *Udinia catori* (Green) (Figure 10a) (Vayssières 2012).

3.5. Circadian rhythms and the importance of ant density on the biological control potential of *O. longinoda*

The ability of *O. longinoda* to protect plants against pests is related to their activity patterns, i.e. the times at which they forage for prey but also on other associated activities, such as patrolling, during which time ant-derived semiochemicals are deposited on leaves, branches and fruits; these semiochemical cues (ant cues) have the potential to act as deterrents to fruit fly pests. In RD Congo, early studies investigating the activity patterns of *O. longinoda* were inconclusive (Dejean 1990), although it was shown that when *O. longinoda* hunted by sight, light intensity was crucial and other parameters such as temperature and humidity also played an important role (Dejean 1986). Study of the circadian activity patterns of *O. longinoda* and the influence of particular ecological factors on this activity is of great interest because it affords an opportunity to understand what drives the spatiotemporal distribution of *O. longinoda* in trees and in orchards. In Benin, preliminary results indicate that circadian activity of *O. longinoda* is continuous (Figure 11) although diurnal activity is greater than nocturnal activity (Vayssières et al. 2011b). In the South Sudan Beninese zone, there seems to be no difference in *O. longinoda* activity between dry, rainy and harmattan seasons (Vayssières et al. 2011b). However, this may be different in the North Sudan and South Sahelian zones and requires further study.

Oecophylla longinoda density is crucial for biological control. The effectiveness of both *Oecophylla* species in controlling insect pests was positively correlated with high ant abundance on host trees (Van Mele et al. 2007; Peng and Christian 2008). For this reason, *O. longinoda* abundance is a key factor, which should be regularly monitored to determine the optimal density for biological control. Various methods used to assess ant densities have been tested in Benin including three methods based on the number of ant trails on the main branches of a tree (called the Peng 1, Peng 2 and Offenberg indices) and one method based on the number of ant nests per tree. According to Wargui et al. (2015), nest counting is not recommended, whereas the Peng 1 index can track dynamics at low ant abundances and the Peng 2 and Offenberg indices can be used in most situations. The number of nests fluctuated widely suggested that their number was unlikely to reflect ant abundance, but rather the influence of tree phenology on nest-building behaviour (Wargui et al. 2015).

4. *Oecophylla smaragdina,* as a biological control agent in Southern Asia through to Northern Australia

In a 1992 review the two species, *O. smaragdina* and *O. longinoda*, were reported to effectively protect eight crops against different insect pests in many countries (Way and Khoo 1992). In a more recent review covering studies made between 2004 and 2014, the two species were shown to protect nine different crops against a number of different pests in eight different countries (Offenberg 2015). By combining previous reviews Peng and Christian (2004) were able to show that the two *Oecophylla* species controlled more than 50 different pest species in more than 12 different crops. However, the biological control potential of *Oecophylla* species is far better known in Asia than in Africa; research on *O. smaragdina* and the use of this ant for biological control is much more advanced in South East Asia and Australia than research on *O. longinoda* in Africa. Having said that, the use of *O. longinoda* in Africa is currently increasing, particularly in organic cashew, cocoa and mango production (Van Mele and Vayssières 2007a). Of particular relevance, the prey of *O. longinoda* includes fruit flies and these ants are increasingly being recognized as successful endemic natural enemies of fruit flies in mango (Peng and Christian 2006; Van Mele et al. 2007; Vayssières et al. 2013).

Oecophylla smaragdina is one of the most ancient biological control agents used against insect pests on citrus (Groff and Howard 1924). Old Chinese records report that *O. smaragdina* nests were being gathered, sold and established in citrus trees to control insect pests over 1700 years ago (Chen 1962). Chinese growers in the Canton area are still using *O. smaragdina* to control *Tesseratoma papillosa* (Drury) (Hemiptera Tessaratomidae) on lychees (*Litchi chinensis* Sonn.) (Jianzhong 1990). In the Mekong Delta of Vietnam, there is also a long tradition of *O. smaragdina* husbandry (Barzman et al. 1996; Van Mele and Cuc 2000). In Australia, *O. smaragdina* is currently used in biological control programmes against pests on cashew (Peng et al. 1995), mango (Peng and Christian 2005a) and mahogany, *Swietenia macophylla* King (Peng et al. 2011). In South-East Asian citrus plantations, *O. smaragdina* effectively controls many insects including key pests such as citrus bugs, *Rhynchocoris humeralis* (Thunberg), the aphids *Toxoptera aurantii* (Boyer de Fonscolombe) and *Toxoptera citricidus* (Kirkaldy), leaf-miners *Phyllocnistis citrella* Stainton and the weevil *Hypomeces squamosus* (Fabricius) (Groff and Howard 1925; Yang 1982; Huang and Yang 1987; Barzman et al. 1996; Van Mele and Van Lenteren 2002; Offenberg et al. 2013).

In Australian mango plantations, *O. smaragdina* effectively controls thrips *Selenothrips rubrocinctus* (Giard), leafhoppers *Idioscopus nitidulus* (Walker), the fruit fly, *Bactrocera jarvisi* (Tryon), mango seed weevils *Sternochetus mangiferae* (Fabricius) and mango bugs *Campylomma austrina* Malipatil (Peng and Christian 2004, 2005b, 2006, 2007, 2008). However, it has also been reported that *O. smaragdina* was unable to protect mango (Thai variety) against the leafhopper *Ideoscopus clypealis* (Lethierry) in Thailand (Offenberg et al. 2013). In Australian cashew plantations *O. smaragdina* effectively controls key pests such as the cashew bug *Helopeltis pernicialis* Stonedahl Malipatil & Houston, the fruit-spotting bug, *Amblypelta lutescens lutescens* Distant and also the moth *Anigraea ochrobasis* (Hampson) (Peng et al. 1997a, b; Peng and Christian 2005c).

5. *Oecophylla longinoda,* as a biological control agent in sub-Saharan Africa

In sub-Saharan Africa, the history of using *O. longinoda* to control insect pests is relatively new compared with South East Asia. There are reports of *O. longinoda* significantly reducing damage in cocoa due to *Distantiella theobroma* (Distant) (Room 1971; Majer 1972), and in coconut due to *Pseudotheraptus wayi* Brown (Simmonds 1924 ; Way 1951, 1953; Vanderplank 1960). Studies in Ghana have also shown that the presence of *O. longinoda* reduces the incidence of two serious diseases of cocoa that are transmitted by a mirid bug and they suggest that this was because *O. longinoda* workers were efficient in capturing phytophagous insects, especially the cacao mirid bugs (Leston 1973).

Recently *O. longinoda* has become more widely accepted as a precious biological control tool in Ghana, Guinea, Tanzania, Senegal and Benin (Ativor et al. 2012; Olutu et al. 2013; Diamé et al. 2015; Anato et al. 2015). In Ghana, Dwomoh et al. (2008) demonstrated that *O. longinoda* controlled sap-sucking bugs in cashew plamtations, even though the ants caused some disturbance to farmers during harvest. Studies in Benin demonstrated that the presence of *O. longinoda* reduced the incidence of pests such as cashew bugs (Figure 12a) (Anato et al. 2015) and mango seed weevils (Figure 12b) in orchards (Vayssières et al. unpublished data).

In Benin, *O. longinoda* was shown to be of economic significance in protecting mango orchards against fruit flies (Van Mele et al. 2007) even though predation of tephritid adults is, globally, rarely observed (Figure 13a, b, c, d). The repulsive effect of 'ant-cues' left on the fruits are far more important than the predation issue (Vayssières et al. 2013). Unfortunately, about 50% of the mango pickers considered *O. longinoda* as a nuisance (Sinzogan et al. 2008) and this percentage was even higher in some other West African countries such as Côte-d'Ivoire, Mali and Senegal among others (Diamé et al. 2015). Between 2009 and 2012, the West African Fruit Fly Initiative (WAFFI: a regional control programme to develop and promote area-wide integrated fruit fly management in West Africa), began to reverse this trend using regional participatory approaches. Adverse perceptions have now been revised and there is currently a more positive attitude towards *O. longinoda* in Ghana and Benin (Ouagoussounon et al. 2015). Consequently, *O. longinoda* has been included as an integral component within Integrated Pest Management (IPM) strategies against fruit pests in some West and East African countries (Dwomoh et al. 2008; Vayssières et al. 2011b; Seguni et al. 2011; Abdulla et al. 2015).

After a first article demonstrating a key role for *O. longinoda* in mango orchards in Benin (Van Mele et al. 2007), subsequent field and laboratory studies have elucidated the tritrophic interactions between mangoes, the two fruit fly species *B. dorsalis* and *C. cosyra*, and *O. longinoda*. Laboratory experiments showed that: (a) fruit flies landed significantly more often on fruits of ant-free trees than on fruits from ant-colonized trees (Figure 14); (b) time spent on mangoes was significantly lower for fruits on which ants had previously foraged and deposited ant cues (Figure 15); (c) ant cues inhibited fruit fly oviposition behaviour (Figure 16); (d) the concentration of ant-cues was significantly negatively correlated with the number of fruit fly pupae collected per kg fruit (Table 3 and Table 4) as was the distance from ant-nests (Figure 17) (Adandonon et al. 2009; Van Mele et al. 2009a; Vayssières et al. 2013). However, field observations revealed that there was no difference in damage to fruit collected at different distances from ant nests, suggesting that physical or visual mechanisms could complement the deterrent effect of ant cues to fruit flies (Adandonon et al. 2009). Oviposition behaviour seemed to be independent of fruit fly species when ant cues were present, especially after fruit flies have landed on mangoes marked with ant cues (Vayssières et al. 2013). Based on the above studies it can be concluded that the presence of *O. longinoda* in mango orchards reduces the damage caused by tephritid fruit flies by: i) rare predation of adult fruit flies (Figure 13a, b); ii) quite frequent predation of third instar larvae (Figure 18); and especially via, iii) the deterrent effect of ant cues deposited by *O. longinoda* on fruit and other parts of the tree. In Benin, early findings also suggest that ant cues protect fruits of *Citrus sinensis* (L.) Osbeck and *Citrus reticulata* Blanco from *B. dorsalis* oviposition (Wargui, 2010). These studies now need to be repeated on other fruit tree species such as *Citrus paradisi* Macfad., which are also attacked by *B. dorsalis* throughout western Africa.

Because fruit flies are prey for *O. longinoda* it is not surprising that they detect and avoid ant-related semiochemicals, as shown for other herbivores that are preyed upon by ants (Offenberg et al. 2004; Adandonon et al. 2009; Van Mele et al. 2009a; Offenberg 2014). All major groups of arthropods (insects, millipedes and spiders) are captured by *O. longinoda* within their host trees as well as in secondary territories (Figure 19a, b, c, d). Regular weekly monitoring of prey capture and food scavenging activities of *O. longinoda* in a large mango orchard in Benin over two consecutive years (2009-2010) have shown that, in both years, there were similar patterns of insect groups and plant debris recovered in nests (Table 5). During this study a total of 241 species of insects were recovered from ant nests; this included 61 species associated specifically with mango of which 48 were pest species representing 78.7% of the species associated with mango (Vayssières et al. 2015b).

Oecophylla longinoda may not only protect crops against invertebrate pests. A study of the perceptions of mango and cashew growers in Guinea showed that more than half of the growers said that *O. longinoda* helped protect their orchards against theft as people are afraid to be bitten by the ants (Van Mele et al. 2009b). Growers also indicated that *O. longinoda* deterred snakes and regularly mentioned that *O. longinoda* reduced damage by fruit-eating bats; some farmers said that bats disliked the smell of *O. longinoda* (Van Mele et al. 2009b). Another advantage is the improvement of physicochemical, microbiological and organoleptic properties of mangoes picked in Benin from trees with *O. longinoda* nests compared with fruit picked from trees without *O. longinoda* (Houngbo 2011).

Effects of *O. longinoda* may not only be positive as they may have negative effects on other beneficial species. An important issue to consider is the potential predation and disturbance of tephritid parasitoids (Hymenoptera: Braconidae) by *O. longinoda*. This has long been a point of discussion by colleagues involved in fruit fly biological control using parasitoids. However, during our own field studies (2005-2012) in all the agroecological zones of Benin, we never saw any predation of parasitoids (*Fopius* species, *Psyttalia* species, *Diachasmimorpha* species) by *O. longinoda* (Vayssières et al., unpublished data). Adult parasitoids were often observed foraging on the same mango fruits as ant workers without the ants attacking them. In confined conditions, however, the results could be quite different: presence of *O. longinoda* inhibiting the activity of *Fopius arisanus* (Sonan) has been observed (Appiah et al. 2014). According to Aluja and Birk (2003), however, valid conclusions should only be deduced from experiments carried out under natural conditions (vs confined conditions). Furthermore, Peng and Christian (2013) showed that *O. longinoda*, in the field, either benefited or had no impact on natural enemy diversity and abundance. They argued that ants improved the health of their host trees and that this enhanced subsequent conditions thereby attracting more arthropods, including natural enemies of pests.

Other ant species than *O. longinoda* may also have potential as biological control agents in orchards. Throughout the world, examples of benefits from ants as predators of fruit pests have been demonstrated. In Brazil, for example, *Pheidole* species are important predators of *Anastrepha* species (Fernandes et al. 2012) and in south Morocco, the ant *Monomorium subopacum* Mayr was by far the most efficient predator of larvae of the fruit fly *C. capitata*, under argan trees (*Argania spinosa* (L.) Skeels) (El Keroumia et al. 2010). Also the ant *Wasmania auropunctata* Roger has been observed to protect cocoa from pests in Cameroon (Bruneau De Miré 1969) and the ant *Dolichoderus thoracicus* (Smith) has been observed to protect sapodilla, *Manilkara sapota* (L.) from pests in Vietnam (Van Mele and Cuc 2001).

6. Research gaps

6.1 Main research interests

Some of the most important research topics that must be covered in order to develop and improve the use of *O. longinoda* in tropical African agriculture are: (i) characterizing the genetic structure of different *O. longinoda* populations in Africa and their agroecological diversity because some ant populations seem to be more efficient predators than others); (ii) characterizing the semiochemical deposits made by ants and quantifying the persistence of their deterrent properties against fruit flies and other pests; (iii) developing methods to conserve and increase *O. longinoda* populations when conditions are suboptimal; (iv) assessing the feasibility of *O. longinoda* as biological control agents in more crops; (v) elucidating the mechanisms behind the improvement of physicochemical, microbiological and organoleptic properties of mangoes picked from mango trees with *O. longinoda*; and lastly (vi) mapping the main factors influencing the activity patterns of *O. longinoda* in relation to the different agroecological zones. The latter point is especially important for West Africa where WAFFI is encouraging the use of *O. longinoda* within IPM strategies.

6.2 Additional research interests

Apart from their biological control activities, *O. smaragdina* are also used in South East Asia as edible insect protein and as a healthy human food (Offenberg et al. 2010; Offenberg 2011; Van Huis et al. 2013; Van Itterbeck 2014), and also in traditional medicine (Chen and Alue 1994; Oudhia 2002). These services should also be investigated for *O. longinoda* throughout sub-Saharan Africa.

7. Conclusion

Since 2005 we have suggested that the use of *O. longinoda* colonies for biological control seems well suited for perennial cropping systems in Benin because these generalist predators are constantly available, widespread, effective and efficient against many tree pests, and self-regenerating (Vayssières 2007; Ouagoussounon et al. 2013; Anato et al. 2015; Wargui et al. 2015; Vayssières et al. 2015b). In this review we have shown that *O. longinoda* can enhance both the quality and quantity of fruit production in mango (Van Mele et al. 2007) and cashew orchards (Anato et al. 2015) and preliminary experiments in Benin have shown that similar effects may also be achieved in citrus orchards (Wargui 2010). Furthermore, emerging African markets for organic and sustainably-managed fruit and nut production may promote further interest in the use of *O. longinoda* (Van Mele and Vayssières 2007b). Other African countries such as Ghana (Dwomoh et al. 2008), Senegal (Diamé et al. 2015) and Tanzania

(Abdulla et al. 2015; Kirkegaard et al., 2015) are also increasing research on the applied aspects of *O. longinoda* and are providing interesting new results (Table 6).

Long term trends suggest that growing attention is being paid to biological control and particularly the use of *O. longinoda* (Table 7). Following successful biological control campaigns against the cassava mealybug, *Phenococcus manihoti* Matile-Ferrero and the mango mealybug, *Rastrococcus invadens* Williams in Africa in the 1980s (Herren and Neuenschwander 1991; Neuenschwander, 2003), confidence in this technology has increased resulting in new investment into classical biological control. Accordingly, records of publications on biological control increased four-fold between the early 1980s and the early 2010s (Table 7). Of these 16 – 25% have dealt with predators. Although ants are one of the most abundant arthropod groups, only about 6% of publications centered on predators address the role of ants. The relative proportion of records dealing with ants in conjunction with biological control remained rather stable; about 10% of publications on predators are devoted to *Oecophylla* species, predominantly *O. smaragdina* (Figure 20). All these data came from CAB Abstracts database subsets and were adjusted for potential overlap between biological control and ecology.

Oecophylla longinoda could offer a valuable and substantial contribution to biological control and IPM of fruit flies. The knowledge is incomplete and seems to be restricted, for the moment, to Ghana, Tanzania and Benin. Recommendations should be provided to growers throughout sub-Saharan Africa who want to use *O. longinoda* as a tool in conservation biological control. According to Offenberg (2015), both *O. longinoda* and *O. smaragdina* provide examples of documented and efficient conservation biological control. To better exploit their biological control activities, protection of *O. longinoda* colonies in fruit plantations in the African savannahs and forests should be promoted in stakeholder awareness campains across sub-Saharan Africa. Moreover, considering all the additional benefits (physicochemical, microbiological, organoleptic, food, medicinal properties) this should really be a primary goal.

Lastly, we would like to draw attention to the tremendous deforestation of tropical forests and savannas, which inexorably leads to irreversible losses in biodiversity (Ahrends et al. 2010; Norris et al. 2010; Sodhi et al. 2009). Protection of tropical forests and savannas is crucial to halt biodiversity losses, but also, more specifically, to protect *O. longinoda,* which can provide so many services to mankind.

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Dedication

This chapter is dedicated to our friend and colleague, Serge Quilici, who always encouraged our activities with the greatest enthusiasm, generosity and practical assistance.

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Jean-François Vayssières (PhD-HDR) is a senior entomologist attached to the Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD) in Montpellier (France) specializing in agricultural entomology. Previously he worked in La Réunion, French Guiana and West Africa, including Benin where he was based at the International Institute of Tropical Agriculture IITA for 11 years. His research interests include ecology of pest-natural enemy complexes on tropical fruits (food web structure) and biodiversity issues. He has been involved in regional IPM projects focused on fruit fly management such as the ‘Regional control program against the Carambola Fruit Fly’ in South America.

Joachim Offenberg (PhD) is senior researcher at Aarhus University in Denmark, specializing in ant-plant interactions. Since 2001 he has been studying tropical weaver ants and how they can be used in agriculture, including pest control, nutrient dynamics between ants and plants, and the utilization of ant larvae as a source of edible protein. Currently these research topics are also being addressed with temperate ants in temperate agriculture. He has published more than 50 peer reviewed scientific papers on ants and their interactions with plants and works as an associated editor for the journal, Asian Myrmecology.

Antonio Sinzogan (PhD) is a *Beta-gamma* scientist (Beta stand for biological sciences and gamma for social sciences) working in the area of agricultural crop protection research. He has more than ten-years experience as a field researcher and university lecturer, a good understanding of what is required for managing team research and a good scientific publication record. Current research interests include using innovative agricultural research to provide viable methods for moving towards sustainable integrated pest management (IPM). This involves linking various technologies (developed jointly with farmers) to parallel capacity building, thereby ensuring long lasting benefits at both the farm and community level. The crops concerned are mango and cotton and the control methods involved are IPM with natural pesticides (neem in conjunction with GF120 lures) and natural enemies (weaver ants).

Appolinaire Adandonon (PhD) is an Assistant Professor at the University of Agriculture of Kétou, specializing in Crop Protection and with a focus on plant pathology and agricultural entomology. For the past ten years his research interests have not only been on the incidence and integrated management and reduction of fruit fly damage in West Africa but also on pests and diseases of other crops including citrus, *Jatropha*, soybean, cowpea and mango. Through the West African Fruit Fly Initiative project he conducted applied research on the development of fruit fly control technologies in eight West African countries. He currently coordinates, at the national level, a technology dissemination project on control of fruit flies in the Republic of Benin. He has published a number of papers and book chapters on fruit flies. He is a reviewer for many journals including the Journal of Applied Biosciences, Crop Protection, European Journal of Plant Pathology, Global Research Journal of Microbiology, Journal of Agricultural Sciences and African Plant Protection.

Rosine Brisso Wargui (PhD) is a research entomologist specializing in crop science, agricultural entomology, and with an emphasis on Integrated Pest Management on perennial tree crops. She graduated in January 2016 at the University of Abomey-Calavi, Benin. Previously, she worked as a research assistant at the International Institute of Tropical Agriculture (IITA) on the West African Fruit Fly Initiative (WAFFI). Her research focuses on the use of weaver ants, *Oecophylla longinoda* Latreille (Hymenoptera: Formicidae), for biological control of insect pests associated with economically important fruit crop species in Benin.

Florence Mahouton Anato (PhD) is a young entomologist who has worked with various insect species since 2006. Her main field of expertise is biological control using parasitoïds and predators. She has worked on rice stem borer, termites and fruit flies at AfricaRice and the International Institute of Tropical Agriculture (IITA), Benin. For her PhD degree, she studied biological control of pests on mango and cashew using weaver ants as part of the project 'Increasing value of African mango and cashew' based in the University of Abomey-Calavi, Benin.

Hermance Yénoukounmey Houngbo (Msc) is currently a PhD student working in food technology and nutrition. She graduated with her Masters degree in food quality control and technology from the University of Abomey Calavi, Benin in November 2012. Previously, she worked as a research assistant on nutritional, microbiological and chemical quality of mango fruits protected by weaver ants, as part of the project 'Increasing value of African mango and cashew' based in the University of Africa Calavi, Benin. Her work focuses on possible impacts on fruit quality of the use of weaver ants for biological control of fruits flies in mango orchards.

Issa Ouagoussounon (PhD) is a young entomologist specializing in crop science and agricultural entomology. He graduated in January 2016 at the University of Abomey-Calavi, Benin. Previously, he worked as a research assistant at the International Institute of Tropical Agriculture (IITA) on the West African Fruit Fly Initiative (WAFFI) and, in Belgium, on aphid glycosyl hydrolase inhibitors. His research focuses on strategies to improve rearing methods for colonies of the weaver ant, *Oecophylla longinoda* Latreille (Hymenoptera: Formicidae), for use in biological control of fruit flies in Benin.

Lamine Diame (PhD) received his PhD in Ecology and Ecosystems Management from Cheikh Anta Diop University, Dakar, Senegal, and previously a Masters degree in Management of Horticultural Agroecosystems from the same university. His main field of expertise is with the ant fauna of Sahelian ecosystems and their use in biological control, with a particular emphasis on use of the weaver ant, *Oecophylla longinida*, for control of fruit flies. His research includes characterization of Senegalese agroecosystems in relation to fruit fly populations.

Serge Quilici (PhD-HDR) was a senior entomologist attached to the Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD) in Montpellier (France) specializing in agricultural entomology. Based in La Réunion, he was a world renowned expert on fruit flies and contributed significantly to improve the scientific knowledge on the biology and ecology of this important taxonomic group. He was a longstanding member of the international committee of the International Congress of Fruit Flies and the ’Conférence Internationale Francophone d’Entomologie’ (CIFE). He was also an international expert working for Ministère de l’Agriculture, de l’Agro-alimentaire et de la Forêt (MAAF), the International Atomic Energy Agency (IAEA) and the United States Department for Agriculture (USDA). Serge Quilici has always been very concerned by the practical application of his results, so he engaged early in his carrer with promoting integrated pest management, especially within the International Organisation of Biological Control (IOBC). His profound entomological knowledge allowed him to develop bio-technical methods for improving trapping systems and biological control approaches by successfully establishing hymenopteran parasitoids. As a passionate naturalist, he was personaly engaged in several committees of the Ministry of Environment and was also active in nature conservation.

Jean-Yves Rey (PhD) is a senior agronomist attached to the Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD) in Montpellier, France. He graduated from the Ecole Nationale Supérieure d’Horticulture de Versailles and did his PhD at the University of Montpellier II. Although currently based in Senegal at the Institut Sénégalais de Recherche Agricole, he has worked in various countries in West and Central Africa on tropical fruit crops for more than 45 years. His research interests concern the improvement of sustainable fruit tree-based systems, particularly the relationships between the design and management of orchards and the effects of pests and diseases.

Georg Goergen (PhD) is a research entomologist at the International Institute of Tropical Agriculture. He joined in 1987 to work on a biological control programme against the cassava mealybug under the framework of a PhD fellowship. Over a 20-year period based at the IITA station Cotonou, Benin, he has established an institutional taxonomic capacity building programme to study arthropods of agricultural importance with a particular focus on biological control of pests introduced into tropical Africa. His professional experience and research interests are in the field of integrated pest management, habitat management and biodiversity of afrotropical insects including Tephritid flies.

Marc De Meyer (PhD) is an entomologist attached to the Royal Museum for Central Africa in Tervuren (Belgium). Previously he worked in Botswana and Kenya for a number of years. His main field of expertise is the taxonomy and systematics of selected groups of Diptera such as Pipunculidae, Syrphidae and Tephritidae, with emphasis on the Afrotropical fauna. His research includes different aspects, from taxonomic revisions to studies on evolutionary trends and speciation events.

Paul Van Mele (PhD) is an agricultural scientist who obtained his PhD in 2000 from Wageningen University on fruit farmers' knowledge and innovations with regard to integrated pest management. He currently runs his own business, Agro-Insight (Belgium), making training videos for farmers in developing countries. He is co-founder of the international NGO Access Agriculture that enables south-south exchange of and access to quality audio-visual training materials to support smallholder farmers.

Table 1: Food web in mango orchards in Benin

PRIMARY LEVEL	SECONDARY LEVEL	
Main fruit-hosts	**Tephritidae**	**Insect parasitoids**
Mangifera indica L. (mango)	*Bactrocera dorsalis* (Hendel)	*Pachycrepoideus vindemiae* (Rondani
Terminalia catappa L. (tropical almond)		*Fopius arisanus* (Sonan)
mango	*Ceratitis cosyra* (Walker)	*Fopius caudatus* (Szépligeti)
mango		*Psyttalia cosyrae* (Wilkinson)
mango		*Psyttalia concolor* Szépligeti
mango		*Diachasmimorpha fullawayi* (Silvestr
mango		*Tetrastichus giffardianus* Silvestri
Sarcocephalus latifolius (Smith) Bruce (African peach)		*F. caudatus*
Psidium guajava L. (common guava)		*F. caudatus*
Annona senegalensis Pers. (wild custard apple)		*F. caudatus*
wild custard apple		*Psyttalia perproxima* (Silvestrii)
Anacardium occidentale L. (cashew)		*P. vindemiae*
mango	*Ceratitis silvestrii* Bezzi	*F. caudatus*
mango		*P. cosyrae*
Vitellaria paradoxa L. (shea butter tree)		*P. cosyrae*
shea butter tree		*F. caudatus*
mango	*Ceratitis quinaria* (Bezzi)	*P. perproxima*

shea butter tree shea butter tree		*P. perproxima* *F. caudatus*
Capsicum annuum L. (chilli) chilli	*Ceratitis capitata* (Wiedemann)	*D. fullawayi* *T. giffardianus*
mango	*Ceratitis fasciventris* (Bezzi)	*T. giffardianus*
Citrus sinensis L. (sweet orange)	*Ceratitis ditissima* (Munro)	*Spalangia simplex* Perkins
mango	*Ceratitis anonae* Graham	*T. giffardianus*

Table 2: Main host plants of *Oecophylla longinoda* and their associated trophobionts in Benin

	Host-plant species of *Oecophylla longinoda*		**Associated trophobionts**		
	Family	**Name**	**Name**	**Family**	**Position on the tree**
1	Anacardiaceae	*Mangifera indica* L. (mango)	*Udinia catori* (Green)	Coccidae	on stem (flush) and on fruits
2		*Anacardium occidentale* L. (cashew)	*Parasaissetia nigra* (Nietner)	Coccidae	on stem (flush)
3	Annonaceae	*Monodera tenuifolia* Benth.	*Stictoccocus intermedius* (Newstead)	Stictococcidae	on stem (flush)
4	Apocynaceae	*Holarrhena floribunda* (G. Don) Durand & Schinz	*U. catori*	Coccidae	on stem (flush)
5	Caesalpinioideae	*Isoberlinia doka* Craib & Stapf	*Hilda funesta* (Stal)	Tettigometridae	on stem (flush)
		I. doka	*Coccus hesperidum* (Linnaeus)	Coccidae	on leaves (inside the nest)
6		*Senna siamea* (Lam.) Irwin & Barneby	*Tylococcus westwoodi* Strickland	Pseudococcidae	on stem (flush)
7	Celestraceae	*Maytenus senegalensis* (Lam.) Exell	*Udinia farqharsoni* (Newstead)	Coccidae	on leaves (inside the nest)
8	Chrysobalanaceae	*Maranthes polyandra* (Benth.) Prance	*U. farqharsoni*	Coccidae	on white flowers
9		*Maranthes robusta* (Oliv.) Prance ex F. White	*U. farqharsoni*	Coccidae	on stem (flush)
10	Combretaceae	*Combretum nigricans* Lepr. Ex Guill. & Perr.	*Parasaissetia* sp.	Coccidae	on stem (flush)
		C. nigricans	*Coccus* sp.	Coccidae	on stem (flush)
11	Ebenaceae	*Diospyros mespiliformis* Hochst. Ex A. Rich.	*U. catori*	Coccidae	on stem (flush)
		D. mespiliformis	*U. farqharsoni*	Coccidae	on stem (flush)
12	Euphorbiaceae	*Alchornea cordifolia* [Schumah. & Thonn.] Mûll. Arg.	*T. westwoodi*	Pseudococcidae	on leaves (inside the nest)
		A. cordifolia	*P. nigra*	Coccidae	on stem (flush)
		A. cordifolia	*U. catori*	Coccidae	on leaves (inside the nest)
13	Loganiaceae	*Anthocleista nobilis* G. Don	*Saissetia* sp.	Coccidae	on stem (flush)
14		*Strychnos spinosa* Lam.	*U. farqharsoni*	Coccidae	on stem (flush)

15	Meliaceae	*Khaya senegalensis* (Desr.) A. Juss.	*U. catori*	Coccidae	on leaves (inside the nest)
		K. senegalensis	*U. farqharsoni*	Coccidae	on stem (flush)
		K. senegalensis	*U. catori*	Coccidae	on stem (flush)
16	Mimosoideae	*Acacia auriculiformis* A. Cunn. Ex Benth.	*Coccus* sp	Coccidae	on stem (flush)
17		*Albizia glaberrima* (Schumach. & Thonn.) Benth.	*Oxyrhachis tarandus* Fab.	Membracidae	on stem (flush)
18	Moraceae	*Ficus sur* Forssk.	*U. catori*	Coccidae	on fruits
		F. sur	*H. funesta*	Tettigometridae	on fruits
19		*Ficus vallis-choudae* Del.	*Hilda undata* (Walker)	Tettigometridae	on fruits
20	Myrtaceae	*Psidium guajava* L. (common guava)	*P. nigra*	Coccidae	on stem (flush)
		common guava	*U. catori*	Coccidae	on leaves (inside the nest)
21		*Syzygium guineense* (Willd.) DC.	*U. catori*	Coccidae	on stem (flush)
22	Ochnaceae	*Lophira lanceolata* Van Tiegh. ex Kay	*U. catori*	Coccidae	on leaves (inside the nest)
		L. lanceolata	*P. nigra*	Coccidae	on stem (flush)
23	Rubiaceae	*Aidia genipiflora* (DC.) Dandy	*U. farqharsoni*	Coccidae	on leaves (inside the nest)
24		*Gardenia erubescens* Stapf & Hutch.	*P. nigra*	Coccidae	on fruits
		G. erubescens	*Saissetia privigna* De Lotto	Coccidae	on fruits
		G. erubescens	*Planococcus kenyae* (Le Pellay)	Pseudococcidae	on fruits
25		*Psydrax horizontalis* (Schumach. & Thonn.) Bridson	*U. farqharsoni*	Coccidae	on stem of this liana
26		*Sarcocephalus latifolius* (Smilth) Bruce	*P. nigra*	Coccidae	on leaves (inside the nest)
		S. latifolius	*H. funesta*	Tettigometridae	on stem (flush)
		S. latifolius	*H. undata*	Tettigometridae	on stem (flush)
		S. latifolius	*Parasaissetia* sp.	Coccidae	on stem (flush)
27	Rutaceae	*Citrus limon* (L.) Burm. F. (lemon)	*Coccus hesperidum* (Linnaeus)	Coccidae	on stem (flush)
28		*Citrus sinensis* (L.) Osbeck (sweet orange)	*C. hesperidum*	Coccidae	on stem (flush)
29	Sapindaceae	*Paullinia pinnata* L.	*T. westwoodi*	Pseudococcidae	on leaves (inside the nest)
30		*Blighia unijugata* Haker	*P. nigra*	Coccidae	on stem (flush)
31		*Lecaniodiscus cupanioides* Planch. Ex Benth.	*C. hesperidum*	Coccidae	on stem (flush)
32	Sapotaceae	*Vitellaria paradoxa* Gaertn. F. (shea butter tree)	*U. catori*	Coccidae	on leaves (inside the nest)
		shea butter tree	*Parasaissetia* sp.	Coccidae	on stem (flush)
33	Simaroubaceae	*Hannoa undulata* (Guill. & Perr.) Planch.	*U. catori*	Coccidae	on stem (flush)
34	Verbenaceae	*Vitex doniana* Sweet	*U. catori*	Coccidae	on leaves (inside the nest)

Table 3: Number of fruit fly pupae present in mangoes in relation to the density of ant pheromone sources in a choice test (n = 20).

		Number of pupae (*B. dorsalis* and *C. cosyra*) per kg of mango fruits[3]	
Treatment[1]		Initial[2]	Final
d < 1 m		0	8.73 ± 1.74 a
1 m < d < 3 m		0	25.41 ± 2.16 b
no ants		0	53.61 ± 4.17 c

[1] Mango fruits were collected from fruits with *Oecophylla* within 1 m and 1-3 m distance from ant nests, as well as from trees without *Oecophylla*. The three treatments were put in the same cage and offered to tephritids for 72h oviposition.

[2] Fruits unconfined to tephritids were incubated for pupae emergence to test initial field infestation (Initial) while pupae emerging from 72h fly-oviposited fruits was considered as greenhouse infestation (Final).

[3] Interaction between treatment and fly species was not significant ($P = 0.05$). Each value is a mean (± SE) of 20 replicates. In the same column, values followed by a different letter are significantly different ($P < 0.05$) according to Student-Newman Keuls test (Adandonon et al. 2009).

Table 4: Fruit fly damage of ant-marked and unmarked fruits

		Number of pupae per kg of mango fruits		
Treatment		Initial[1]	Final	
			B. dorsalis	*C. cosyra*
Oecophylla -marked		0	9.65 ± 1.33 c	10.28 ± 1.34 c
Unmarked		0	65.04 ± 3.19 a	44.88 ± 3.32 b

[1] Number of pupae from mangoes collected in the orchard and incubated for initial infestation. Each value is a mean (± SE) of 10 replicates. In the same column, values followed by a different letter are significantly different ($P < 0.05$) according to GLM using Student-Newman Keuls test (Adandonon et al. 2009).

Table 5: Relationship between the mango fruit developmental stages and the insect groups and plant debris recovered from *Oecophylla longinoda* nests (from Vayssières et al. 2015)

Fruit Stage		Hymeno	Hemiptera	Isoptera	Coleoptera	Diptera	Other_insects	Debris	TOTAL_Contents	Temp	RH
	N	Mean ± S.E	Mean ± S.E	Mean ± S.E	Mean ± S.E	Mean ± S.E	Mean ± S.E	Mean ± S.E	Mean ± S.E	Mean ± S.E	Mean ± S.E
Flowering	11	36.3 ± 7.0 b	0.3 ± 0.2 c	0.0 ± 0.0 c	0.2 ± 0.2 d	0.6 ± 0.2 c	25.6 ± 8.2 cd	39.0 ± 10.0 a	102.0 ± 10.5 bc	28.4 ± 0.5 b	26.0 ± 2.7 d
Fruit Growing	18	78.1 ± 5.3 a	0.9 ± 0.4 b	0.0 ± 0.0 c	1.8 ± 0.5 c	0.6 ± 0.2 c	16.9 ± 4.0 d	6.0 ± 1.2 b	104.4 ± 7.3 bc	31.3 ± 0.5 a	40.0 ± 2.9 c
Pre-Maturity	6	27.7 ± 8.2 b	6.7 ± 1.6 a	3.0 ± 2.6 ab	4.0 ± 1.5 bc	4.2 ± 1.4 b	34.5 ± 11.4 bc	0.8 ± 0.4 c	80.8 ± 15.9 c	31.2 ± 1.2 a	54.8 ± 6.4 bc
Maturity	27	15.4 ± 2.6 c	4.7 ± 1.1 a	6.7 ± 2.0 a	26.2 ± 4.4 a	28.6 ± 3.5 a	71.4 ± 9.0 a	0.1 ± 0.1 c	153.0 ± 9.9 a	28.2 ± 0.4 b	71.7 ± 1.7 a
Without Fruit	42	13.2 ± 2.3 c	2.1 ± 0.4 b	2.9 ± 0.9 b	4.6 ± 0.9 b	2.0 ± 0.4 b	58.6 ± 7.0 ab	52.1 ± 8.4 a	135.5 ± 7.7 ab	27.6 ± 0.2 b	60.0 ± 2.8 b
F-value (4, 53)		26,07	6,33	4,85	21,05	56,37	18,59	11,03	5,00	11,48	18,05
P-value		< 0.0001	0,0003	0,0021	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0,0017	< 0.0001	< 0.0001

Linear correlations between different six groups of insect species, plant debris and also between insect species - debris and abiotic factors (temperature and relative humidity) in relation to different mango tree stages. In the same column, values followed by a different letter are significantly different (P < 0.05) according to ANOVA (Vayssières et al. 2015).

Table 6: Synthesis of research in the last forty years on *Oecophylla* species as beneficial predators

Crop	Ant species	Country	Pest	Pest reduction	Damage reduction	Yield increase	Quality improved	Relation with orchard type	Co al
Mango	*O. longinoda*	Senegal	*Bactrocera dorsalis* (Hendel)	+	+	+		+	
	O. longinoda	Benin	*B. dorsalis, Ceratitis cosyra* (Walker)	+	+	+			
	O. longinoda	Benin	*B. dorsalis, C. cosyra*	+	+				
	O. longinoda	Benin	*B. dorsalis, C. cosyra*	+	+		+		
	O. smaragdina	Thailand	*Idioscopus clypealis* (Lethierry)	-	-	-			
	O. smaragdina	Australia	*Bactrocera jarvisi* (Tryon)	+	+	+			
	O. smaragdina	Australia	*Sternochetus mangiferae* (Fabricius)	+	+	+			
	O. smaragdina	Australia	several mango pests	+	+	+			
	O. smaragdina	Australia	*Campylomma austrina* Malipatil	+	+	+			
	O. smaragdina	Australia	Mealybugs	-	-				
	O. smaragdina	India	several mango pests (*B. dorsalis* included)	+	+	+			
Citrus	*O. longinoda*	Ghana	*B. dorsalis, Ceratitis ditissima* (Munro)	+	+	+			
	O. longinoda	Benin	*B. dorsalis*	+	+				
	O. smaragdina	Thailand	*Hypomeces squamosus* (Fabricius)	+	+	n			
	O. smaragdina	Vietnam	pest species not specified	+	+	+			
	O. smaragdina	India	several citrus pests	+	+	+			
	O. smaragdina	Vietnam	several citrus pests						
	O. smaragdina	China	*Tessaratoma papillosa* (Drury) & other Heteroptera	+	+	+			
	O. smaragdina	China	*Rhynchoris humeralis* (Thnb.)	+	+	+			
Cashew	*O. longinoda*	Benin	*Anoplocnemis curvipes* (Fabricius); *Helopeltis schoutedeni* Reuter; *Mirperus jaculus* (Thnb.); *Pseudotheraptus devastans* (Distant); *Tupalus fasciatus* (Dallas)	+	+	+	+		
	O. longinoda	Ghana	*A. curvipes*; *H. schoutedeni; P. devastans*	+	+	+			
	O. longinoda	Ghana	*A. curvipes*; *H. schoutedeni; P. devastans*	+	+	+			
	O. longinoda	Tanzania	*Helopeltis* spp.; *Pseudotheraptus wayi* Brown	+	+				
	O. smaragdina	Australia	*Helopeltis pernicialis* Stonedahl; *Solenothrips rubrocinctus* (Giard) and other cashew pests	+	+	+			

Table 7: Changes in the number of publications related to biological control and particularly the use of weaver ants over time (CAB abstracts)

KEYWORDS	1965-1969	1970-1974	1975-1979	1980-1984	1985-1989	1990- 1994	1995-199
BIOLOGICAL CONTROL	186	6 575	13 134	16 404	23 479	27 065	27 393
PREDATOR	59	1 665	3 424	3 902	5 776	6 197	6 548
ANT & BIOLOGICAL CONTROL	2	106	234	311	394	377	373
Both *OECOPHYLLA* SPECIES	0	15	25	18	20	23	40
OECOPHYLLA LONGINODA	0	7	15	6	3	10	13
OECOPHYLLA SMARAGDINA	0	8	10	12	17	13	27

Figure 1: Worldwide distribution of the genus *Oecophylla* species (*O. longinoda* in orange, *O. smaragdina* in blue)

Figure 2: *Oecophylla longinoda* (Georg Goergen credit).

Figure 3: a) *O. smaragdina*, b) *O. smaragdina* detail of mandibles (Kim Aaen credit)

Figure 4: Nests of *O. longinoda* on fruit trees: a) mango, b) grapefruit, c) cashew, d) guava (Jean-François Vayssières credit)

Figure 5: Nest of *O. longinoda* on shrubs: a) *Antidesma venosum*, b) *Sarcocephalus latifolius* (Jean-François Vayssières credit).

Figure 6: Different life stages of *O. longinoda* on mango (Jean-François Vayssières credit) a) queen, b) males with small and large workers.

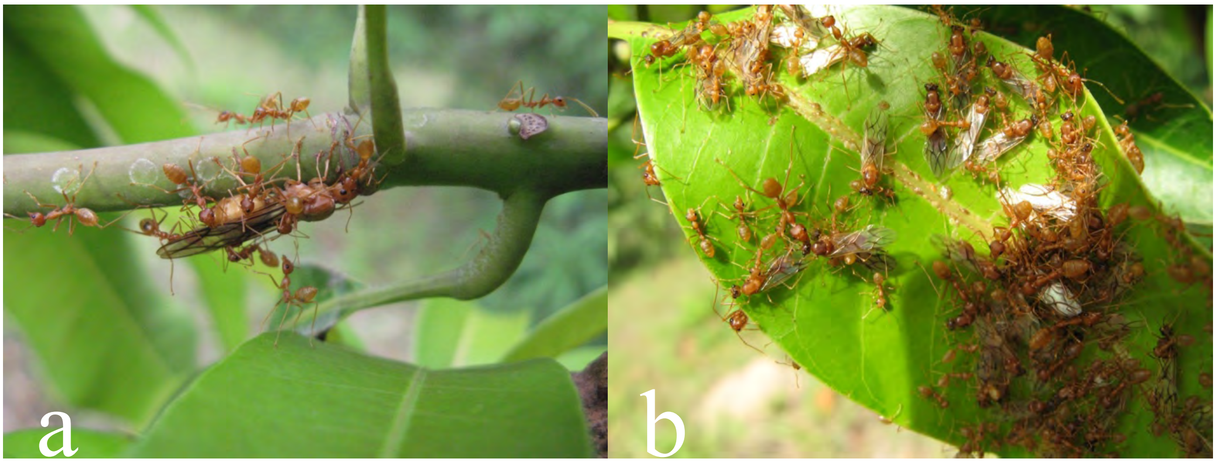


Figure 7: Construction of a nest using the last larval instar (Jean-François Vayssières credit).

Figure 8: Artificial nest on mango (Jean-François Vayssières credit).

Figure 9: Plant material harvested and carried back to the nest along the trunk of a mango tree (Jean-François Vayssières credit) a) Harvested seed; b) Detail of seed being carried to the nest; c) Harvested plant debris.

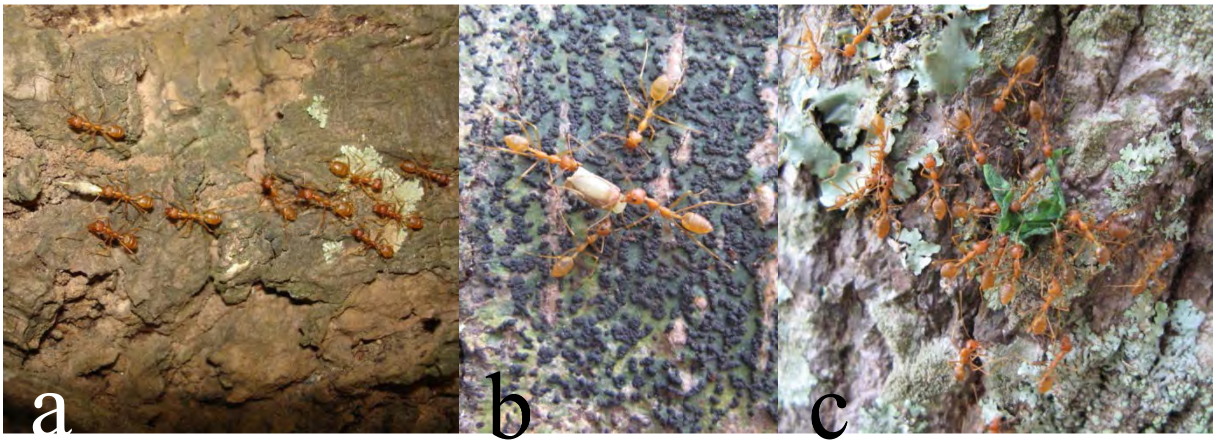
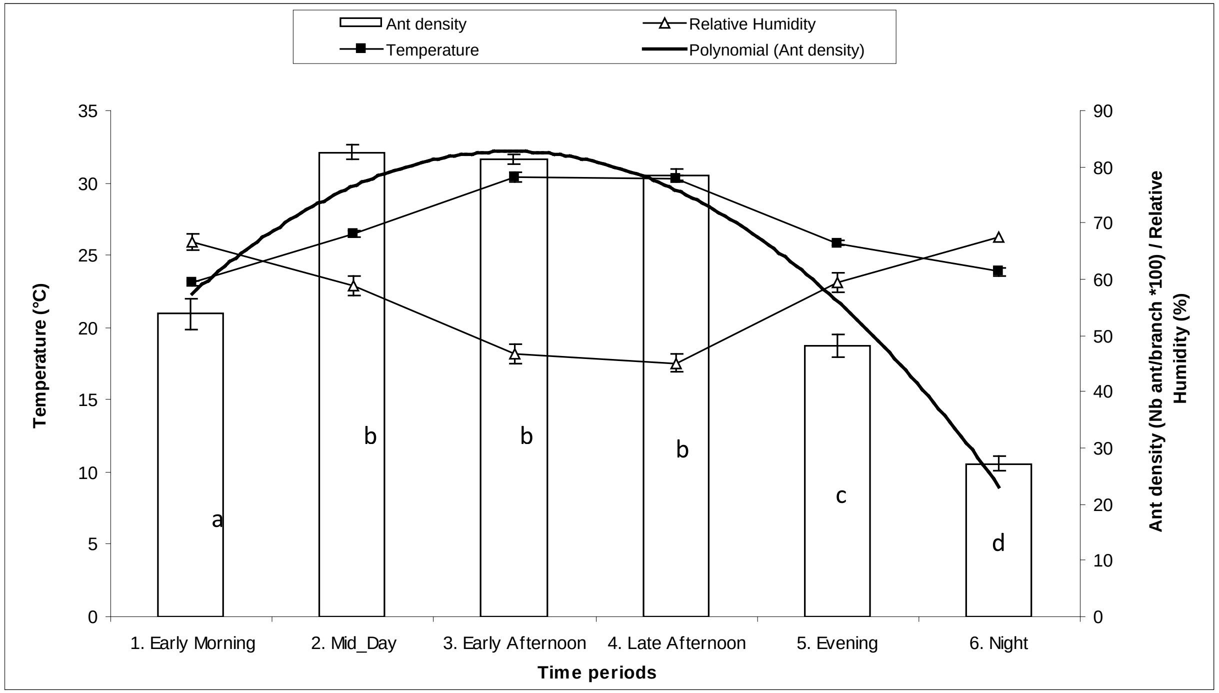


Figure 10: *O. longinoda* attending: a) *Udinia catori* (Hem.: Coccidae) on mango and b) *Hilda* sp. (Hem.: Tettigometridae) on *Albizia glaberrima* (Jean-François Vayssières credit).

Figure 11: Mean diurnal rhythms of activity of *Oecophylla longinoda* outside the nest in relation to variation in temperature and humidity



Each observation for each of the different factors (ant density, temperature and humidity) is the mean ± SE of observations made hourly from 7:30 AM to 6:30 AM the following day, carried out on a fortnightly basis for two years and pooled according to the following time periods: 1. Early Morning (5:30 AM to 8:30 AM); 2. Mid-Day (9:30 AM to 11:30 AM); 3. Early Afternoon (12:30 PM to 2:30 PM); 4. Late Afternoon (3:30 PM to 6:30 PM); 5. Evening (7:30 PM to 10:30 PM); 6. Night (11:30 PM to 4:30 AM). Bar charts with a different letter are significantly different ($P < 0.05$). The polynomial curve line is the software-derived trend for the bar chart (Vayssières et al. 2011).

Figure 12: *O. longinoda* capturing: a) *Sternochetus mangiferae* (Col.) on a mango (Department of Atlantique, Benin) and b) *Pseudotheraptus devastans* (Hem.: Coreidae) on cashew flowers (Department of Borgou, Benin) (Jean-François Vayssières credit).

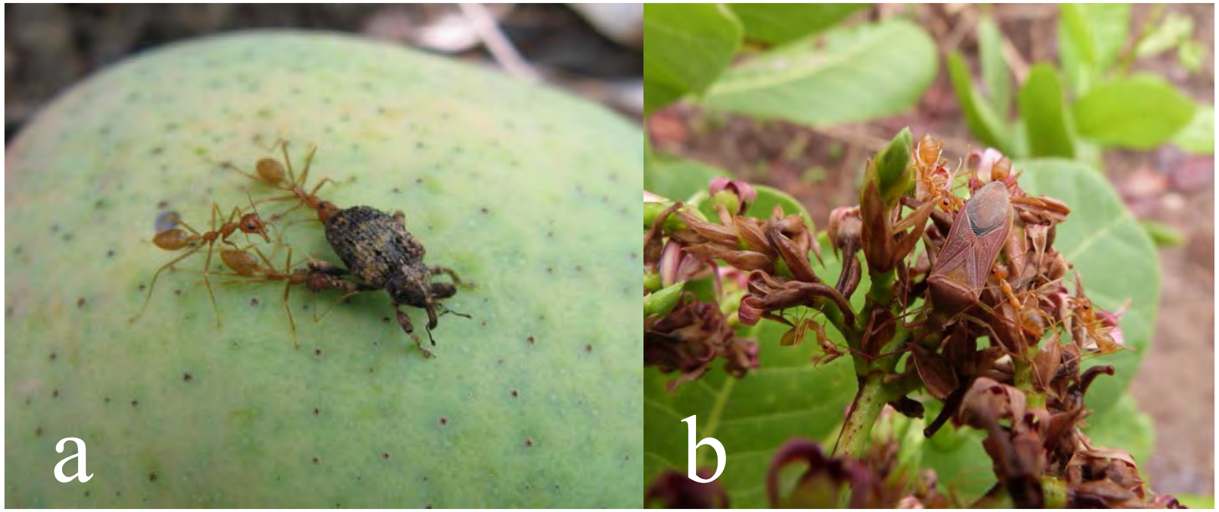


Figure 13: *Ceratitis cosyra* male during the same sequence (a, b) and females (c, d) captured on mango by *O. longinoda* (Department of Borgou, Benin) (Jean-François Vayssières credit).

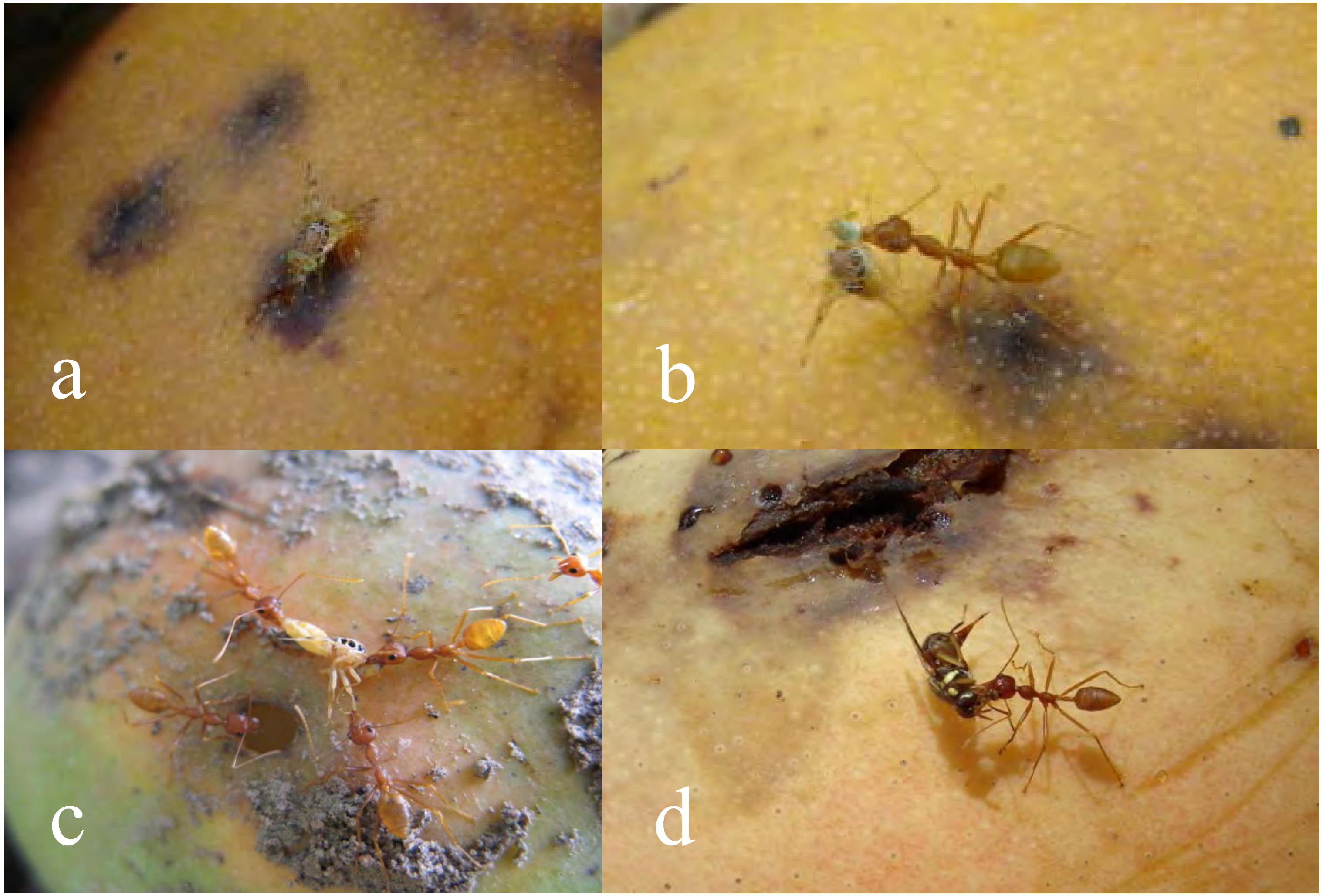


Figure 14: Number of occasions that a fruitfly landed on mangoes in relation to ant treatment (mangoes that were exposed or unexposed to *O. longinoda*). Interactions between treatment and fruit fly species, *B. dorsalis* and *C. cosyra,* were not significant (*P* = 0.05), hence data were pooled. Data are the mean ± SE.

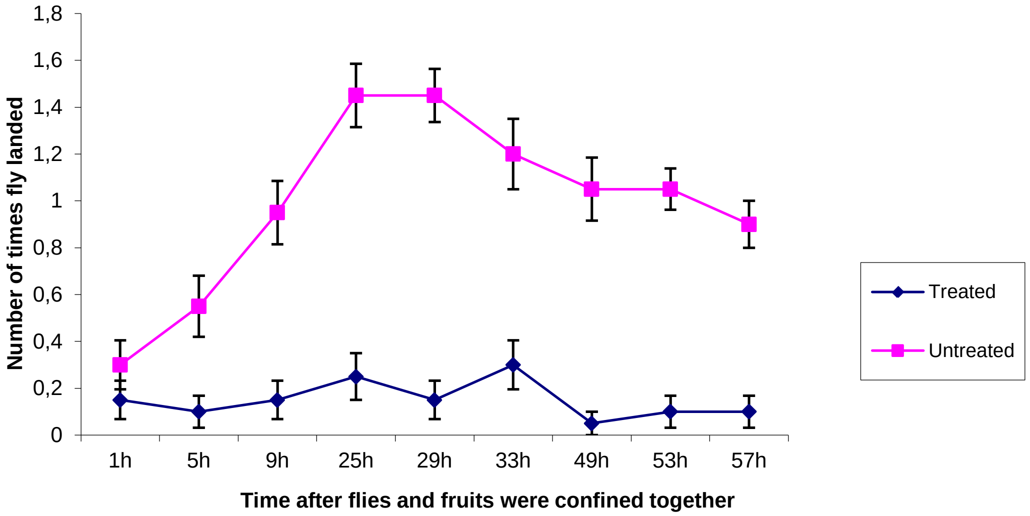


Figure 15: Time spent, per fruit fly, walking on mangoes in relation to ant treatment (mangoes that were exposed or unexposed to *O. longinoda*). Interactions between treatment and fruit fly species, *B. dorsalis* and *C. cosyra,* were not significant (P = 0.05). Data are the mean ± SE.

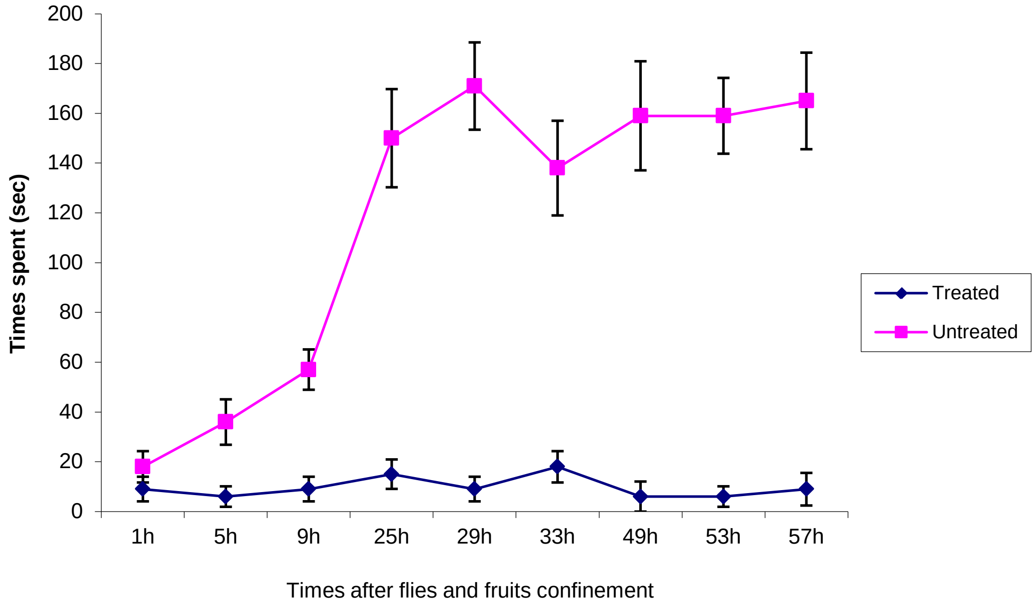


Figure 16: Time to first fruit fly oviposition attempt to oviposit on mangoes in relation to ant treatment (mangoes that were exposed or unexposed to *O. longinoda*). Interactions between treatment and fruit fly species, *B. dorsalis* and *C. cosyra,* were not significant (*P* = 0.05). Data are the mean ± SE.

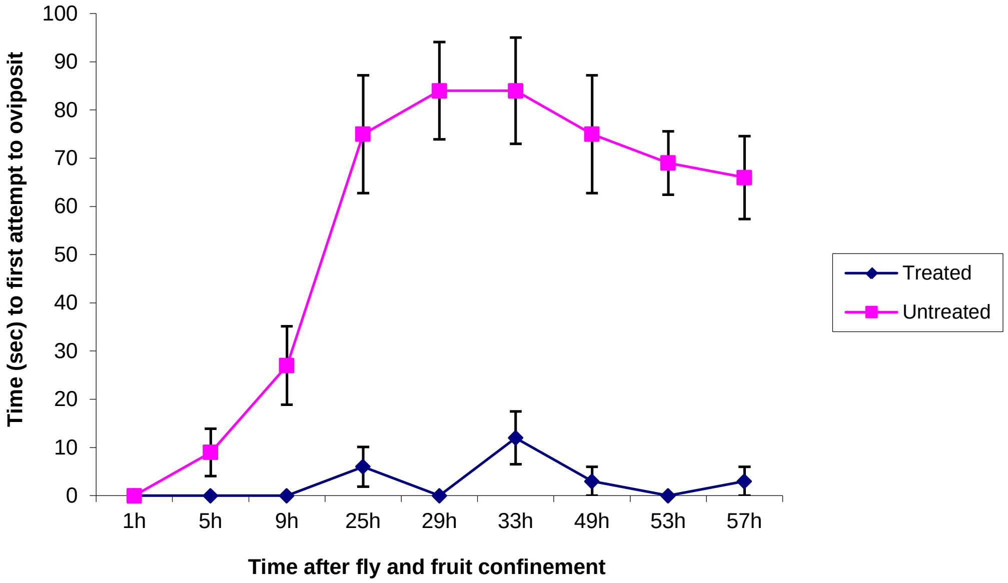


Figure 17: Mean + SE number of *B. dorsalis* pupae per kg fruit in relation to the density of ant pheromone sources. Mango fruits were collected from trees with *O. longinoda* within 1 m and 1–3 m distance from ant nests, as well as from trees without *O. longinoda*. In the choice test, fruit flies were offered the three mangoes at the same time, whereas in the no-choice test, flies were offered fruit from one treatment at a time.

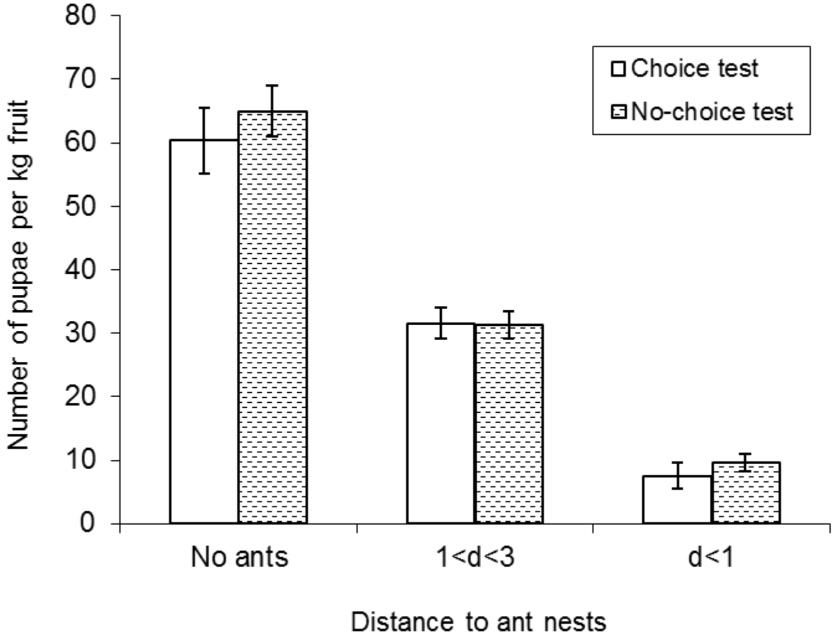


Figure 18: Tephritid larvae captured on a mango (cv Eldon) by *O. longinoda* (Department of Borgou, Benin) (Jean-François Vayssières credit).

Figure 19: *O. longinoda* capturing: a) *Pachycondyla* sp. (Hym.: Formicidae) on a mango tree, b) *Dysdercus* sp. (Hem.: Pyrrhocoreidae) on a mango (also with a *Dorylus* sp. to the left), c) Nitidulidae (Col.) on a mango, d) larva of *Euschmidtia* sp. (Orth.: Euschmidtiidae) under a mango tree (Jean-François Vayssières credit).

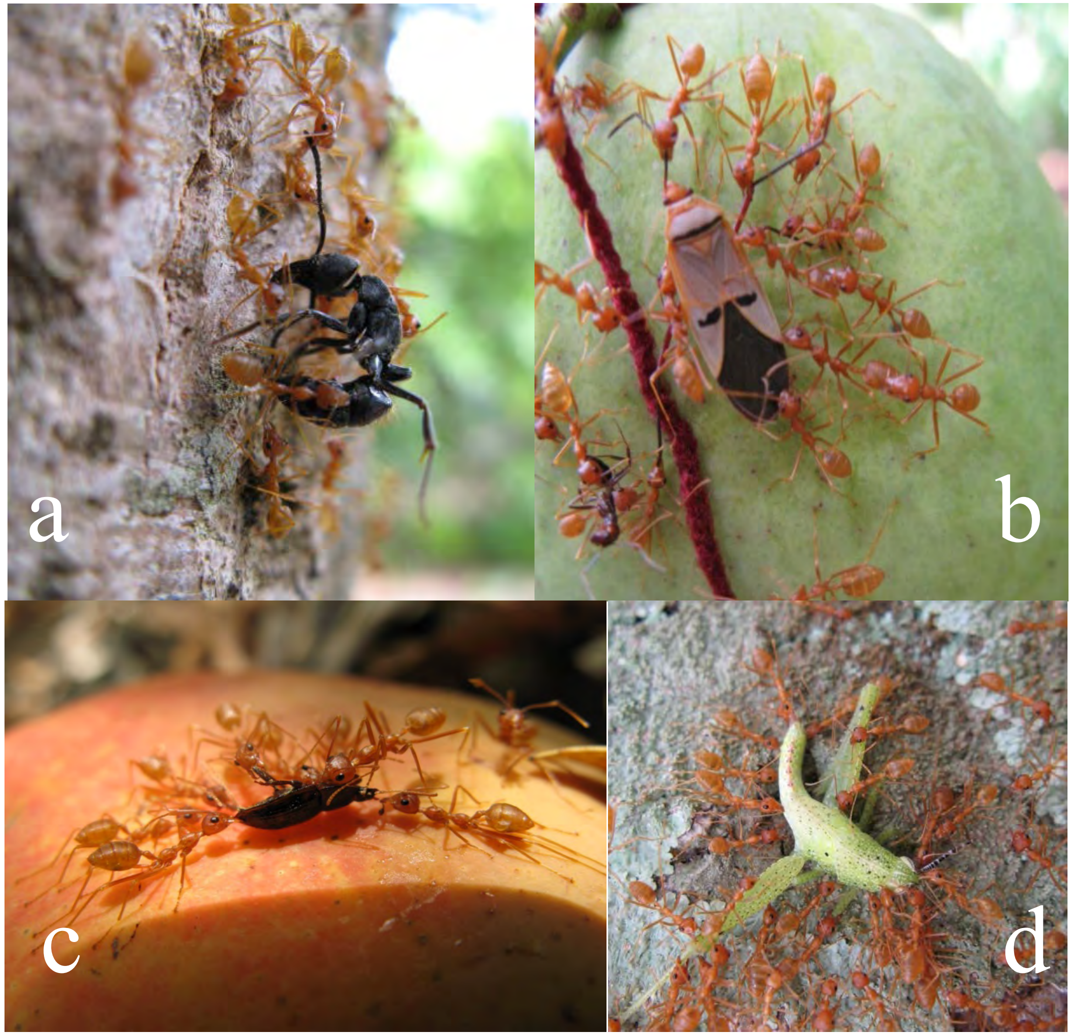


Figure 20: Number of publications relating to *O. longinoda* and *O. smaragdina* in the CAB Abstracts database