



CONTRIBUTION OF ASIAN WEAVER ANTS, *OECOPHYLLA SMARAGDINA* (HYMENOPTERA: FORMICIDAE)) IN DELIVERING DIVERSE ECOSYSTEM SERVICES AND FUNCTIONING IN CHANGING LANDSCAPE: A REVIEW

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ABSTRACT

Ants like weaver ants are among the most abundant arthropod taxa in various ecosystems and provide important ecosystem services. Ants are predators that cause various beneficial and harmful effects to terrestrial ecosystem including agro- ecosystems. Ants play important role in terms of seed dispersal, soil enhancement, scavenging of urban food waste, pest control along with mutualistic interactions. As predators feed on herbivorous pests, there is improvement of biological control that leads to increase in crop yield. But ants also attack and feed on predatory arthropods, key pollinators and crop plants that result in pest outbreaks and reduced flower formation and fruit setting. Among various ants, weaver ants (*Oecophylla smaragdina*) act as major predators which control various economically-damaging pest insects of tropical fruit and nut crops. These ants hosts trophobiont honeydew producers particularly mealybugs, whiteflies, scale insects, aphids etc. which itself act as pests. Moreover, ants supplement their diet with sugars obtained from floral and extrafloral nectaries that bring about physiological cost to the plant. Experimental studies with various treatments using ants confirmed the effects of weaver ants on beneficial and pest insects and tree-crop productivity. Results confirmed that pest reduction is observed on cacao (*Theobroma cacao*), cashew (*Anacardium occidentale*), mango (*Mangifera indica*) trees etc. *Oecophylla* ants provided the valuable ecosystem service in regard to natural method of biological pest control in tropical tree crops. In South-East Asia, *Oecophylla smaragdina* plays a key role in shaping the ecological and evolutionary trajectories of plant–pollinator interactions. *Oecophylla* ants can co-exist well with other beneficial insects, enhance plant productivity along with other ecosystem services. Change in land use, urbanization and climate change affects various ecosystem services provided by these ants.

Keywords: Predators, extrafloral nectaries, pollinators, trophobiont, productivity, pest, ecosystem services.

Introduction

In current scenario of biodiversity decline, the management and valuation of ecosystem services (ES) become the focal point in various conservation and policy strategies. Ecosystem services can be categorized into three main groups: provisioning of material goods, regulation of ecosystem processes (supporting and regulating services), and non-material (cultural) services such as learning and inspiration (Millennium Ecosystem Assessment, 2005; IPBES, 2019). In this regard, ants regarded as one of the most ecologically dominant and adaptable invertebrate taxa plays a crucial role in diverse terrestrial ecosystems like forest ecosystem, agro-ecosystems etc. Ants with more than 14,000 species contribute significantly to invertebrate biomass and ecological processes (Hölldobler & Wilson, 1990). They show diverse behaviours and engage in various interactions ranging from predation to mutualism and thereby have provides notable contribution in terms of crop health and pest regulation (Lach et al., 2010). Ants are involved in various antagonistic interactions like competition, predation, and parasitism along with facilitative and mutualistic interactions where one or both participants receive a net benefit (Bertness and Callaway, 1994; Bruno et al., 2003; Grosholz, 2005; Stachowicz, 2001). Interactions of ants with their partners provide some best examples of the reciprocally beneficial interactions (Bronstein 1998) particularly mutualisms that play vital roles in structuring community composition and functioning (Christian, 2001; Kaplan and Eubanks, 2005; Mooney, 2007; O'Dowd et al. 2003; Poulsen and Currie, 2006; Wimp and Whitham, 2001). Interactions between ants and their partners dates back to 45–60 MYA (Poulsen and Currie, 2006; Stadler and Dixon, 2005). Mutualists provide rewards that increase the survival and reproduction of ants with their colonies besides fuelling ants for collecting new resources and involved in aggressive behaviours (Davidson, 1998). The dynamics of ant mutualisms have been the focus of substantive reviews (Bronstein, 1998; Heil and McKey, 2003; insect tending Pierce et al., 2002; Stadler and Dixon, 2005; Way, 1963; seed dispersal in Giladi, 2006; ant–plant symbioses in Davidson and McKey, 1993; Heil and McKey, 2003; and ant–fungi–bacteria in Poulsen and Currie, 2006) and are featured in various books (Beattie, 1985; Rico-Gray and Oliveira, 2007; Stadler and Dixon, 2008). In agricultural systems, ants when act as predators help to control pest populations naturally but they also have the tendency to form mutualistic associations with honeydew-producing insects that enhance pest infestations. In addition to this, ants alter soil properties through nesting and foraging activities that alter nutrient dynamics and overall plant growth. Various researchers have highlighted various beneficial contributions that include improved nutrient cycling process and agricultural pest control along with harmful role including seed damage and crop yield reduction due to promotion of pest outbreaks by defending honeydew-producing insects. In terrestrial ecosystem like agro-ecosystems, ants act as keystone species due to their interactions with various organisms at multiple trophic levels but their ecological roles in changing landscape are least studied. The distinction between beneficial and detrimental species varies with species composition, changing environmental conditions and cropping pattern. In present scenario, sustainable agriculture is the need of the hour and in this regard, ants are being re-investigated for their potential role in reducing chemical inputs thereby enhancing ecosystem services. This review critically examines the diverse ecological services and functions provided by ants particularly Asian weaver ants in changing landscape.

POSITIVE INTERACTION AND BENEFITS

- (a) **In Ecosystem Functioning:** Weaver ants are generalist arthropod predators having complex ecological roles in agroecosystems (Peng et al., 1999, 2014; Van Mele and Cuc, 2000; Peng and Christian, 2004; Pierre and Idris, 2013; Abdulla et al., 2015, 2017; Anato et al., 2017; Forbes and Northfield, 2017). These ants provide beneficial ecosystem services by not only consuming pest insects, but also causes negative services by sheltering other herbivores and form trophobiotic relationships (Offenberg et al., 2013; Forbes and Northfield, 2017), besides preying upon beneficial arthropod predators and pollinators (Gonzalvez et al., 2013; Rodriguez-Girones et al., 2013). Review on various studies in regard to weaver ants negative

role in biological control or pollination to harm crop yields (e.g., Tsuji et al., 2004; Offenberg et al., 2013) are rare and any harm and damage by weaver ants to crops in regard to harvesting homopterans, or deterring predators, parasitoids, and pollinators is outweighed by their net benefits in pest reduction and increased yields.

- (b) **As Ecosystem Engineers:** Role of ants in ecosystems is extensively investigated mainly from the perspective of the effects of ground-dwelling ants on soil processes and function, emphasizing their role as ecosystem engineers. Physical ecosystem engineers are organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials. From various studies, it is clear that ground ants create and modify habitat for other organisms and modulate the availability of resources by creating the biomantle (Johnson, 1990). Investigations show that ants act as ecosystem engineers (Jones et al., 1994; Brussaard et al., 1997). Studies shows that ants facilitate the development of other organisms in their mounds, including unique plants that otherwise would not exist (King, 1977; Folgarait et al., 1996), or increase the amounts of some microorganisms (Czerwinski et al., 1971; Petal, 1980).
- (c) **As Bioindicators of Ecological System:** Due to complexity of most ecological systems, individual species or functionally similar species groups are often employed as bio-indicators of environmental processes (McGoech M.A,1998) and thereby help to identify environmental disturbances and take appropriate actions in due time to reduce damages, mitigate consequences and restore ecosystems. In this regard, ants have been recognised as good indicators of terrestrial ecosystems. Ants started been used as indicators of ecological systems in Australia in the mid 1970's that assess impacts of mining (Majer J.D,1983) and are presently used internationally in assessing different degradations in many ecosystems.
- (d) **Interaction with Natural Agricultural Pests and Biological Pest Control:** Numerous ant species act as effective natural enemies of various agricultural pests by preying and consuming herbivorous insects that threaten crop productivity. *Oecophylla smaragdina* is a keystone predator species, very abundant and broadly distributed throughout tropical South-East Asia and north-east Australia (Crozier et al. 2010) Weaver ants are the oldest documented form of biological control with records of *Oecophylla smaragdina* being conserved for natural pest control in 304 AD China (Way and Khoo, 1992). Weaver ants have the potential to control agricultural pests across many tropical countries, as *Oecophylla smaragdina* (Fabricius) is found in Australia, India, and South-East Asia, and *Oecophylla longinoda* (Latrielle) in Sub-Saharan Africa (Vayssieres et al., 2015; Wetterer, 2017). Use of *Oecophylla smaragdina* (weaver ants) in citrus and cashew orchards for biological pest suppression is well documented (Peng & Christian, 2004). *Oecophylla smaragdina* has been recorded to control over 50 pest species in eight different horticultural crops (Peng and Christian, 2004; Offenberg et al.,2013). These ants besides engaging in direct predation interfere with pest establishment and behaviour, thereby reducing the risk of infestation (Way & Khoo, 1992). These ants show active foraging activities and territorial patrols limiting pest harmful activity. Their continuous presence and patrolling on various plant surfaces reduce feeding rates as well as inhibiting egg-laying tendency by pest species. Earlier reviews of *Oecophylla* spp. confirms its role as biological control agents that successfully manage pests in some situations (Way and Khoo, 1992; Van Mele, 2008; Offenberg, 2015), besides have the potential to improve yields. Studies prove that harmful effects of the ants on other beneficial arthropods is counterbalance various benefits by weaver ants (Delabie, 2001; Bluthgen et al., 2006). Presence of ants significantly reduced pest densities of leaf-footed bugs (Coreidae; Peng et al., 1999; Dwomoh et al., 2009), mirid bugs (Miridae; Peng et al., 1999; Ayenor et al., 2007; Dwomoh et al., 2009; Forbes and Northfield, 2017a), stink bugs (Pentatomidae; Peng et al., 1999; Hosetti and Rudresh, 2012) and fruit flies (Tephritidae; Van Mele et al., 2007; Adandonon et al., 2009; Migani et al., 2017) . Studies confirmed that there are increased pest populations and pest infestation with corresponding decline in crop yields once ants from

excluded from cropping areas. In different parts of Africa and Southeast Asia, these ants are integrated into pest management strategies for controlling pest and thereby provide ecologically sound alternative to synthetic pesticides. In absence of mutualistic association with honeydew-producing insects, these ants may act synergistically with other biological control agents such as parasitoids and predatory insects and thereby have profound impact on pest populations. Studies confirmed that harmful effects caused by weaver ants to crops in terms of harvesting homopterans, or deterring predators, parasitoids, and pollinators is outweighed by benefits that ants provide in pest reduction and increased yields.(Tsuji et al., 2004; Offenberger et al., 2013)

- (e) **Soil Aeration and Nutrient Cycling:** Ants play a crucial role in shaping soil structural properties and fertility status through their nesting and foraging behavioral activities. Creation and excavation of tunnels by ants increases not only soil porosity but also enhances both soil aeration and water infiltration (Folgarait, 1998). These physical modifications helps in mixing soil particles with organic material, availability of essential nutrients etc. which overall improve conditions for root growth and microbial colonization. Ant nests act as localized nutrient reservoirs rich in nitrogen and phosphorus that benefit nearby plant roots. They are involved in seed dispersal (myrmecochory) process which contributes to plant regeneration. Additionally, ants are involved in various soil-engineering activities like fragmentation of litter, mixing it into the soil, promote microbial activity, accelerate decomposition of organic matter and improve overall biological health of soil. These diverse activities of ants are particularly important in restoration of degraded lands where there is limited nutrients.
- (f) **Mutualistic Interactions with Plants:** Few ant species show mutualistic interactions with plants that bear extrafloral nectaries or provides food rewards. In return for these resources, ants often provide protection against various herbivorous insects, forming a defense-based mutualism (Heil & McKey, 2003). Many plant species have evolved various strategies to allure ants through such morphological and biochemical traits benefiting plants from reduced herbivore pressure and increased crop productivity. Crops namely cotton, pigeon pea etc. possess extrafloral nectaries which attract predatory ants and thereby suppresses pest population. The success of invasive ants is thought to be linked to the availability of carbohydrate-rich resources, though reports of invasive ant visits to EFNs are mixed as in two laboratory experiments, results reveal that ants cannot induce *Acacia saligna* extrafloral nectar production, but workers of both native and invasive ant species can benefit from extrafloral nectar as they benefit from sucrose (Lach et al., 2009). There are specific ant species which defend various trees from damaging effects of herbivores leading to overall improved tree health and yield. Interactions between ant species and host plants may not always result in positive outcomes as in few cases, ant repel pollinators or interfere with reproductive processes causing reduced crop yield. Proper management of ant-plant mutualistic interactions when integrated into pest management systems can enhance crop resilience and causes reduce reliance on chemical pesticides.
- (g) **In Sustainable Agriculture:** Conservation of natural vegetation and ecological corridors can improve ant-mediated ecosystem services. Identification and promotion of native, predatory ant species in agro- ecosystems involves management practices like maintenance of proper ground cover, intercropping, limited applications of chemical inputs etc. Regular monitoring of ant activity including foraging pattern can be integrated with sustainable pest and soil health management. Farmer when trained to distinguish harmful and beneficial ant species will help in making better decision at the field level.

NEGATIVE INTERACTIONS AND DETRIMENTAL EFFECTS

- (a) **Protection to Honey Producing Pest:** Ants forms mutualistic association with honeydew-producing pests such as aphids, mealybugs, whiteflies, and scale insects. In return for the sugary secretions called honeydew, ants not only provide protection to

these sap-feeding insects but also defend them from natural enemies like parasitoids and predatory beetles (Styrsky & Eubanks, 2007). Such type of protective behavior by ants causes increased survival and reproduction of pest leading to crop damage. In this way, ants may actively attack beneficial insects like parasitoid wasps that are responsible for regulating pest populations which is accompanied by spread of certain plant pathogens. Weaver ants (*Oecophylla* spp.) are recorded to harvest nectar from their host plant, while also “farming” trophobionts like soft scales (Coccidae) and mealybugs (Pseudococcidae) (Bluthgen and Fiedler, 2002). An assessment of the effectiveness of *Oecophylla* ants in controlling insect pest assemblages showed that, except for some honeydew producing pests, the ants were able to control all the main pests of cashew and mango in Australia (Peng and Christian 2005; Peng et al. 2004), of citrus in Vietnam (Van Mele and Cuc, 2003), and of cocoa and coconuts in Papua New Guinea, the Solomon Islands, Tanzania, and Ghana (Stapley 1980; Way and Khoo 1992).. Highlighting such type of mutualisms is critical for maintaining ecological balance in terrestrial ecosystem like agro-ecosystems and thereby helps in successful implementation of IPM strategies.

- (b) **Crop Damage:** Most ant species are not herbivorous but there are certain ants which inflict direct damage to agricultural crops by interfere with flowering and fruit setting besides damaging germinating seeds and young seedlings, leading to poor crop establishment and reduced stand density. Environmental stressor like drought tends to compel ants to feed on sugar-rich plant tissues or harvest developing fruits as resource requirement. In granary, few ant species build nests which thereby reducing food quality and hygiene of the agricultural produce. Besides indirect effects caused by ants, various direct damages can pose economic risks and need serious monitoring in vulnerable cropping systems where there is dominance of ants.
- (c) **Plant-Pollinator Interactions:** Ants are abundant in most diverse habitats. They are opportunistic foragers which consume flower nectar as available (Herrera, Herrera & Espadaler, 1984). Certain ant species are able to displace, through interference or exploitation competition other visitors of flower (Lach, 2007, 2008). Ants have direct effects on plant pollination success, damaging flowers during nectar consumption (Galen & Geib, 2007), and indirect effects that are mediated by changes in pollinator behaviour. These indirect effects can be negative (Ness, 2006) or positive (Altshuler, 1999) in regard to plant reproduction. *O. smaragdina* workers repel pollinators from *Nephelium lappaceum* (Tsuji et al. 2004) and pollen thieves from *Melastoma malabathricum* (Gonzalvez et al. 2013), while they are also active hunters of fig wasps (Ranganathan & Borges, 2009). Ants had a negative effects on pollinator visit rate (Tsuji et al., 2004; Gonzalvez et al., 2013), *O. smaragdina* ants are found to raid bee nests (Seeley, 1983) as they use flowers as hunting platforms. *O. smaragdina* ants are ubiquitous and mobile (Crozier et al. 2010) and also have the potential to affect the relationships between plants and their pollinators at both ecological and evolutionary time-scales, as predicted from recent model studies (Suttle, 2003; Abbott, 2010; Higginson, Ruxton & Skelhorn 2010; Jones, 2010; Rodríguez- Girones, 2012). Studies suggested that pollinators avoid *O. smaragdina* ants, showing behavioural responses similar to those used to avoid other ambush predators (Tsuji et al. 2004; Gonzalvez et al. 2013). *O. smaragdina* ants also reduce the pollination success of *Nephelium lappaceum* because pollinators avoid plants with ant nests (Tsuji et al. 2004). In the case of *M. malabathricum*, however, the pollinators actually prefer plants with ant nests, leading to higher fruit set and seed set as compared to plants without ant nests (Gonzalvez et al. 2013). Flowers of many plants produce ant-repellent substances to prevent ants from consuming their nectar (Junker & Bluthgen, 2008) or have tendency to scare their pollinators (Willmer & Stone, 1997). The production of ant repellents by flowers of various plant species (Willmer & Stone, 1997) and American (Raine, Willmer & Stone, 2002) confirms that ants interfere with the pollination process. The structure and stability of different ecological communities

predicted from study of a single type of interactions, such as predator–prey or plant–pollinator interactions, but from studies of the complex interplay of them all (Melian et al., 2009). The presence of ants at flowers not only alters the foraging behaviour of bees but also affect the relationship of a plant with its flower visitors, and thereby modulating the evolution of flower traits (Gonzalvez et al. 2013).

- (d) **Invasive Ants on Pollination:** Invasive ant species due to their aggressive behaviour can negatively influence agro- ecosystem services by displacing or preying on other beneficial native insects, including pollinators and natural enemies such as parasitoids (Lach, 2007). This will disturbs the ecological balance needed for effective biological control and pollination. *Linepithema humile* (Argentine ant) outcompete native arthropod communities, including key predators and pollinators. Similarly, in citrus orchards, the presence of dominant ant species interfere with the activity of parasitoids which target scale insects and this diminishes the natural biological control strategies of pest infestation. By blocking bees and insects from accessing nectar or pollen, ants affects pollination success accompanied by reduced subsequent fruit set. In areas dominated by aggressive ant species, the foraging activity of honey bees is reduced appreciably. In this regard, there should be proper management in regard to abundance and species composition of ants so that key ecosystem services are never compromised.

RESEARCH GAPS AND FUTURE DIRECTIONS

In spite of various studies in regard to recognition of ants as important ecological agents various terrestrial ecosystems, several critical knowledge gaps persist as majority of present studies are short-term and geographically limited besides focusing on few crop species. There is a need for long-term, multi-crop field studies for evaluation of both ecological functions as well as economic trade-offs. Elaborate studies need to be done in regard to advances in molecular biology so as to unravel complex species interactions and trophic relationships that exist involving ants. Little work has been done in regard to association of microbial communities with ants and their possible role in pest regulation and maintenance of plant health. In regard to changing climate, systematic investigation in terms of ant behaviour, distribution, and ecosystem functions need to be properly explored. There is need to carry out more studies of impacts of ant on plant–pollinator pairs along with community-level studies, using the comparative method for tracing the evolution of ant repellents across plant lineages. Moreover, there is need to evaluate in near future whether African and American ant species use flowers as hunting platforms in the way that *O. smaragdina* ants do.

CONCLUSION

Weaver ants cause diverse roles within ecosystem. In agro-ecosystems, the ants bring about overall influence on crop. It provides varied ecological services like natural pest regulation and soil fertility enhancement besides have the potential to foster pest outbreaks through mutualisms with honeydew-producing insects. Ants can serve as natural allies that reduce reliance on chemical inputs like pesticides besides improving ecosystem resilience. There is need to develop holistic ant management strategy so as to achieve sustainable agriculture. Due to accelerated climate change, there is urgent need for sustainable food systems for which role of ants in agriculture is properly exploited for agro-ecological transformation.

Ants like weaver ants have various impacts on the physical properties, chemical composition, and biodiversity of soils through the construction of complex nest structures in the canopy of various height, extensive food collection and distribution besides multiple mutualistics associations with other organisms. They are regarded as ecosystem engineers and service providers that promote biodiversity, produces resilient ecosystem, rings about sustainable natural resource management along with promotion of healthy ecosystems.

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