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Review

A Review on Distribution Pattern, Nesting Style, Mating Behavior, Colony Organization of Asian weaver ant *Oecophylla smaragdina* (Hymenoptera: Formicidae) Occupying Strategic Biome-agroforestry Systems of Asia

Exélis Moïse Pierre[1,2*], Ramli Rosli[1]

[1]Institute of Biological Science, Faculty of Science, Universiti Malaya, 50603 Kuala Lumpur, Malaysia; (EMP) exelis.pierre@gmail.com; (RR) rosliramli@um.edu.my
[2]Higher Education and Research Direction, Institution of the « La Collectivité Territoriale de la Martinique (CTM) », Gaston Defferre street- Cluny - CS 30137, 97201 Fort-de-France Martinique
* Correspondence: Exélis MP; Ramli R, Institute of Biological Science, Faculty of Science, Universiti Malaya, 50603 Kuala Lumpur, Malaysia

Significance Statement: This review presented the distribution pattern of the Asian weaver ants (AWA) under diverse strategic biome, agroforestry systems and highlighted the economic inputs, society benefits provided. The latest information on nesting, mating behavior and colony social structure is exposed to assess the existence of scarcity, data gaps. *Oecophylla smaragdina* is a dominant arboreal insect sampled from tropical rainforests, major agricultural crops demonstrating biological control agent (BCA) effective abilities on pests of economic interest. Farming business, nutritious diet delicacies among cultural heritage ethnics, established the species as a conservation-evolution model. Poorly documented mating behaviors, colony bionomics, need further study. Reported disservices on pollinators, counter-productive mutualistic interaction oblige a mandatory evaluation of each crops before any adoption of AWA as a BCA.

Abstract: This review discusses the distribution pattern, nesting style, mating behavior, and colony structure of the Asian weaver ants (*Oecophylla smaragdina*) in Asia. Recent findings suggested that weaver ant occurrences are not only limited to tropical rainforests biome, agroforestry and large monoculture fields, but have encroached human rural habitation including densely populated urban areas. Comparatively, *O. longinoda* and *O. smaragdina* are taxonomically classified as two distinct species, but the main differences between them are strongly dependent on the allopatric nature or geographical speciation of their distribution. Although weaver ants are dominant ubiquitous and conspicuous arboreal insects with a predilection for habitation in trees canopies, viable nests colonies on the ground have been reported in Thailand. *O. smaragdina* usually construct their polydomous nests (multiple satellites nests arrangement within a single host but diverse plants species) by weaving tree-leaves using their larval silk. Knowledge on mating behavior is rudimentary; hence more studies are needed especially in understanding how weather parameters affect nuptial flight swarming act. At the colony organization level, comprehensive reports about minor and major workers contrasts with the poorly documented but significant intermediate size of workers caste. The versatile impact of Asian

Oecophylla is offering important ecological subsistence services to both the nature and humans. This is by combining positive economic implications to food security concern with a provision of organic nutrients for host plants and highly healthful diet enhancer (nourishing-medicinal). Despite its wide presence in large oil palms monoculture, only one report had exposed weaver ants' potential positive ecological impact (i.e. predation on bagworms *Pteroma pendula*) in Southeast Asia.

Keywords: Dispersal range; nesting habitat; reproduction; caste system; ecological dominance

1. Introduction

The Weaver ants are eusocial insects, recognized for their extensive organized nests [1]. This review exposed how weaver ant have made a tremendous contribution to ecosystems in general, emphasizing on the numerous benefits provided in agro-ecosystem services [2]. There are two species of weaver ant in the world: the Asian *Oecophylla smaragdina* [3] and African *Oecophylla longinoda* [4]. Both species were classified within genus *Oecophylla*, the old genus of family Formicidae [5]. The weaver ants are obliging arboreal with a predilection for habiting in trees canopies by weaving leaves to construct their multiple satellite nests in each host plant [1]. It is a generalist predator acting aggressively on numerous arthropods as a source of its diet [6,7]. This species is an absolute territorial insect by establishing clear marked boundaries between colonies with a distinctive nobody else's land pattern of occupation strategy [8,9]. The territorial dominant behavior over others insect species determines the outcome of the colony's distribution, expansion strategies to control new suitable areas leading to successful long term occupation [9]. The compilation of information related to weaver ant's precise distribution, occupation patterns in Asia [3] lends evidence for the dual derived ecological interest and economic importance of the species [9,2]. However, both African [10,11] and Asian species breeding status is deficiently documented [12]. Few reports have evaluated this concern and further investigation on the ecology and potential benefit of the Asian *Oecophylla* as a biological control agent (BCA) in oil palm (*Elaeis guineensis*) industry in Malaysia [13,14] and Indonesia [15,16]. However, to respond to such a need, it is necessary to achieve some practical targets by conducting further field trials to further establish a more comprehensive knowledge of the species in areas that have not yet been explored. The main objectives of the review were: (1) to retrieve reports expressing the wide geographical presence within different biomes systems shown by *O. smaragdina* colonies (Table 1) useful to initiate further study on its adoption as a potential biological control agent of commercial crops, and (2) to convince industry stakeholders of the real benefit that they could obtain from the advent of incorporating weaver ants as a supplementary tool in their sustainable maintenance agenda. The present review intends to explore the various areas that need to be covered to answer some serious doubts (is the weaver ant a reliable and feasible tool) that have prevailed in the industry (2). The main concept of omnipresence of such generalist predators is related to the cheap management cost involved whenever used as a biological control agent or under integrated pest management systems [17,7,18].

This review presented, (i) the biogeographically versatile distribution pattern of the Asian weaver ants under diverse biome with its ecological impact; (ii) summarizes the nesting biology and occupation patterns. The review will also explore the latest information on (iii) mating behavior and colony structure of the caste system in weaver ants. This review focused mostly on *O. smaragdina* than *O. longinoda*. Comparative points were given for relevant topics showing discrepancies', scarcity of reports such as mating behaviors, life cycle stages [19,20] and workers caste differentiation [21].

2. Research methodology for this review

2.1. Search and Assessment Inclusion benchmark.

The review was performed to collate the relevant available published academic literature. Only studies that provided information of both *Oecophylla* species were included in a first selective step. The second step of enriching with broader sources was performed in absence of enough supportive elements based solely on first step criteria. Based on this review title terms, "distribution pattern, nesting style, mating behaviour, colony organization and occupying Strategic Biome-agroforestry Systems of Asia**"** appeared as the most dominant and relevant to substantiate *Oecophylla* ants attributes as a dominant entity. The second step of enriching with broader sources was performed in absence of enough supportive elements based solely on first step criteria. This was necessary to extract publications related only by analogy within solely ants taxonomic (http://info-now.org/ants/AntTaxonHierarchy.php) or scientific classification adhering to the Integrated Taxonomic Information System (ITIS, 2006) regrouping the Formicidae family. Studies written in "bahasa Indonesia", French, Spanish and English were included. We included studies from ecology, many surveys check list from diverse countries, foraging and predation behaviors dominantly oriented on the BCA function of the *Oecophylla* genus. To fulfil the main objective of this review (convince farmers of the benefits provisions), topics of services and disservices of *Oecophylla* ants were given priority in our evaluation. The first point objective is to show the omnipresence of the species in various biome, agroforestry systems up to urban occupation. The ubiquitous factor of weaver ant occupation in a diverse host and geographical range shows the species availability in various ecosystems, indicates its potential low cost for further manipulations in commercial crop plantations. Beside that, the potential answer to the global food security looming crisis with weaver ant inclusion in daily diet orientation (Van Itterbeeck, 2014) is an important element. Finally, BCA and IPM treatments were the culminating subjects of research findings since they provided all location type, biome information. Tables were derived from the most relevant papers describing the associated host plants protection from the pests of economic interest provided by *Oecophylla* ants: among them classified invasive species.

2.2. Literature documentation selection.

We started the literature search by using the keywords "*Oecophylla* ants", "Asian weaver ants", "*Oecophylla smaragdina*", "*Oecophylla longinoda*" from Google search engine. The preliminary relevance of each manuscript was determined by the titles based on the abstracts content. From that initial step, if the content seemed to discuss the topic of present review, we obtained its full reference, including author, year, title, and abstract, for further evaluation. We searched Google Scholar, Web of Science, frequently used databases. Because the two species of *Oecophylla* are rarely evaluated for the bagworms in the oil palm plantations industry, we extended the publication date to 1960 up to 2022 (articles published in the past sixty two years), so that the review is constructed based on both older and the recent literature considering broader information retrieval and synthesis demonstrate better the hypothesis of *Oecophylla* ants as being potent predators for the control of harmful pests. We first applied Google general search engine to obtain different sources of papers by using keywords, "Asian weaver ant distribution", "Asian weaver ants nesting" or added "mating behavior", "social structure", "occupation study" and then copy-paste it in Google Scholar. Whenever we search for the keywords preceded with "Asian weaver ant or African weaver ant" the return results was as high as 19200 and 21800, respectively. The research was fine tune by adding "Scholarly articles" before each keywords. Whenever using a less specific term such as "Asian weaver ants", the search turnover decreased by adding "*O. smaragdina*", "*O. longinoda*" to reach 3140 and 1860 respectively. The potentially relevant articles amounted to an average 150, abide to the intended topic title of this review. For the information filtering and final selection of the manuscripts of interest, the quality and eligibility of published articles selection was achieved strongly by considering the following authors for most topics of study: Hölldobler & Wilson, Peng & Christian, Peng *et al*; Offenberg, Offenberg *et al*, Van Mele, Cuc, Offenberg, Wetterer, Lokkers and Azuma. By reading throw pre-selected or selected articles, we found more experts doing fundamental and applied research that could significantly contribute to the value of this review as follows: Newey, Robson, Crozier, Nielsen for the Asian and Nene, Vayssieres, Rwegasira *et al* and Dejean for the African species, respectively. A majority of the selected articles shown an orientation for applied biological control or integrated management treatment on various pest of economic interest. After initial titles screening, reading the abstracts of an average of over 300 related articles, a total of 143 studies were finally identified as relevant to the tile of this review: "A Review on Distribution Pattern, Nesting Style, Mating Behavior, Colony Organization of Asian weaver ant *Oecophylla smaragdina* (Hymenoptera: Formicidae) Occupying Strategic Biome-agroforestry Systems of Asia." For each selected article in the review, the "Related articles" option available in the GoogleScholar database, helped to identify fast similar studies able to enrich the search for study inclusion in the review. For the final inclusion of identified studies, we scanned through the full-text articles to further evaluate their quality and eligibility by systematically targeting the reputable names of those researchers mentioned above, having a strong record related to the *Oecophylla* ant genus. Four studies dated from the 40s were discarded and only one from 1922 was kept for its relevance.

3. Distribution of *O. smaragdina* and its ecological impact

3.1. Origin, behaviors and habitats

Genus *Oecophylla* was originated from Europe, approximately at the beginning of the tertiary era at the Palearctic region (bio-geographical realm) with a sound extension to other zones resulting from the dramatic climate change of the Eocene-Oligocene period[22,20,23]. The two extant species, i.e. *O. smaragdina* and *O. longinoda*, have attracted tremendous interest in the field of ecology and the evolution of ants, which once had a stringent divergence upon 13 - 11 Ma in the late Miocene. *O. smaragdina* is composed of six subspecies whereas *O. longinoda* is constituted of eight subspecies [23]. [24] was the first to provide a distribution map of the two extant species of the world, and it was later modified by [23].

The definite world distributional limits of *Oecophylla* have been evaluated and revised [3]. The very highly aggressive nature of the ants, which is often so obvious, gives an edge for fieldwork observation due to their easy detection, makes any ecological distribution study of the species ideal [24]. *O. longinoda* and *O. smaragdina* are taxonomically classified as two distinct species [25], but the main differences between them are strongly dependent on the allopatric nature or geographical speciation of their distribution [26,1]. Across Asia and Africa, weaver ants of the genus *Oecophylla* have a dominant presence among other forest insect communities [1]. *O. longinoda* distribution is only concentrated under an extensive section of equatorial Africa [4], whereas *O. smaragdina* distribution ranges from Sri Lanka to the sub-continent India-Pakistan-Bangladesh, Nepal, Bhutan to Asia, South China-Taiwan passing through Southeast Asia (Myanmar, Laos, Cambodia, Vietnam, Thailand, Malaysia, Brunei, Philippines, Indonesia, Singapore) to northern Australia, extending to the western Pacific islands of Fiji, Solomon, and Melanesia [3] (Fig. 1).

O. smaragdina is widely distributed in primary or secondary forests, agroforestry or agro-systems, either in temperate or tropical areas [1]. The Asian weaver ants prefer tree canopies either in forested habitats [27,28,29] or rural and densely populated urban areas [30,31]. The various habitats in which *Oecophylla* develops its established colonies are ranging from rainforest and their edges, riparian woodland and closed-forest, *Eucalyptus* woodland, coastal scrub forest, dry sclerophyll forests to urban parkland, public town park and beachfront (Table 1). They occupy microhabitats such as low vegetation, litters, sieved litter as ground hunters or strays individuals [32]. They provide organic nutrients to the host trees by excreting large quantities of faeces matter on the foliage tops [33,34]. Table 1 shows *O. smaragdina* presence in diverse environments range, tropical forests and large plantations such as oil palm (*Elaeis guineensis*) [13,14] and other crops such as cashew nuts (*Anacardium occidentale*), mango (*Mangifera indica*) [37], rambutan (*Nephelium lappaceum*) [38], sweet orange (*Citrus sinensis*), pomelo (*C. grandis* or *C. maxima*), or lime (*C. aurantifolia*) [39]. They are also recorded in the introduced African mahogany (*Khaya ivorensis* and *Khaya senegalensis*) in Southeast Asia [40,41] and Australia [42].

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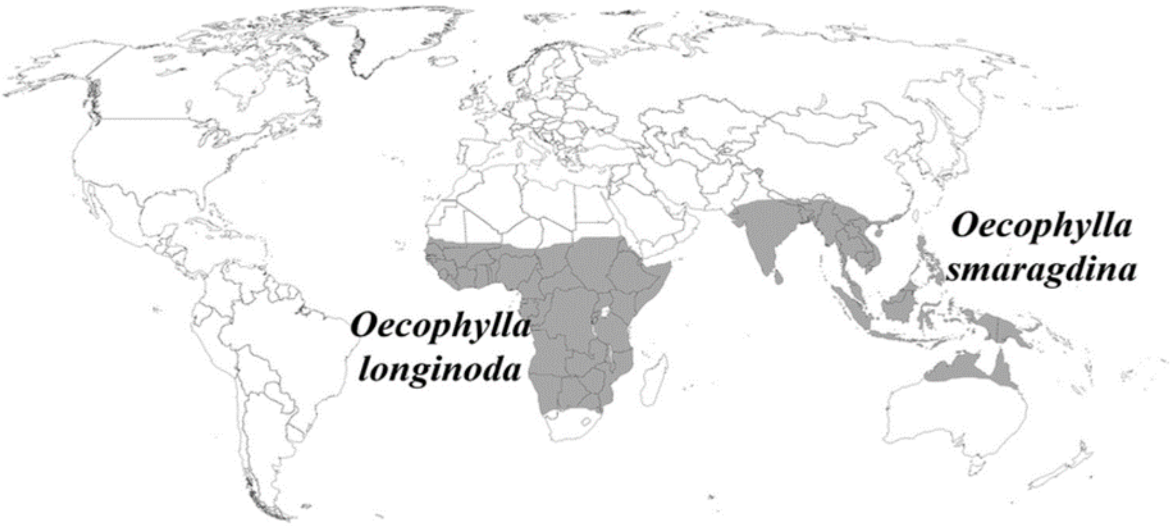

Figure 1. World biogeographically distribution limits of genus *Oecophylla*

A comprehensive world distribution includes many location records taken for the precise positioning of samples. Its occurrences are well documented in various studies in these countries. The task of revising the Asian species included more than 2700 various records [3], whereas the African counterpart species had more than 500 records [4]. [43] the investigation used the Köppen-Geiger system based on climatic apparatus to infer specific ecological requirements for both weaver ant species, which is quite fundamental for research based on official classification purposes. Three main groups, i.e. tropical (A), arid (B), and sub-tropical (C) were derived from this classification.

The availability of the Asian weaver ants on a wide range geographical spatial distribution demonstrate easy access to colonies (table 1) without relying on re-introduction or long distance translocation for biological control application or integrated pest management (IPM), hence providing a cheaper management cost without disturbing biodiversity balance [44,45]. Even though, *O. smaragdina* is a heat tolerant species [1], it also exhibited diverse climatic flexibility comprising tropical, warm semi-arid in India and Australia, dry winter sub-tropical, humid sub-tropical in Southeast Australia and China North, and temperate climates ranging from a multitude of bio-geographical locations in Asia [3]. *O. smaragdina* could be cold-tolerant from a record taken in the Himalaya Northern Nepal-India border, occurring naturally braving winter cold by entering into hibernation ([46] extracted from [3]). Nepal and Indian *Oecophylla* populations are considered much more cold resistant than those of China which needs to be artificially maintained since they stop activity for many weeks during winter season [3]. Table 1 shows ubiquitous distribution of *O. smaragdina* in diverse biome of Asia (biogeographical unit consisting of a biological community sharing regional climate and a variety of habitats) from protected reserve national parks-ecological sanctuaries [47,48], tropical primary rainforests [49,50]. This include agroforestry systems [42,51], large agricultural plantations dominantly under oil palms monoculture system [52,13] to rural and highly modernised populated urban areas [53,30]. An important diversity of host plants are recorded from different field of study i.e. biodiversity check list surveys [54,55] and ethnology investigation on the inclusion of brood weaver ants in native communities

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daily diet [47,56] with their medicinal benefits [57,58]. Some studies looked into behaviours [59,60,61], phylogeography – phylogenetic to assess historical/chronological expansion [19,20] and biological control agent (BCA) efficiency [62].

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Table 1. Biogeographically Distribution and occurrences of *O. smaragdina* in Sub-continent, Nepal-Bhutan

Countries	Location/Geographic coordinates/Biome – environment	Habitat/Associated host plants (Colloquial, Scientific name) – Ants locality common name – Ecosystem services*	References
Sub-continent Sri Lanka	Coconut triangle zone near Colombo. Low rainfall, dry and intermediate climatic zone. Central Sri Lanka, Nochchiyagama 27 km east of Anuradhapura. Wet zone Delgoda Udupila, Gampaha district (07°00 395'N, 0′ 80° 00 96'E). Wet zone	Coconut (*Cocos nucifera*)/ dimiya in Sinhala –BCA Cashew Nuts (*Anacardium occidentale*) - BCA Cashew Nuts (*A. occidentale*) - BCA	[63] [64] [65]
India	Mettupatti, Meenatshipuram, Thirumanickam and Thadaiyampatti and urban disturbed habitats. Madurai District, Tamil Nadu (9′93°N, 78′12°E). Less disturbed rural villages consisting of agricultural fields, riverine areas.Delhi, Patiala, and Agra – urban areas Himalayan mountains of Surinsar Jammu & Kashmir state North India: mountains primary forests – undisturbed highland subtropical dry winter climate University of Agricultural Sciences (UAS) campus in Bangalore & Indian Institute of Technology Madras (IITM) campus in Chennai 12°59′29″N, 80°14′1″E – urban area / undisturbed large strips of native vegetation National Institute of Rourkela, Odisha (22′25ºN, 84′90ºE)	Mango (*Mangifera indica*), neem (*Azadirachta indica*), pongame oiltree (*Pongamia pinnata*), *Citrus* acids / red ants or tonge or babuk – Survey Asian Spatial distribution of the species *Ficus*, *Citrus*, and *Azadirachta*. Colony distribution pattern in relation to biotic & abiotic factors Neem (*A. indica*) and jackfruit tree (*Artocarpus heterophyllus*). Foraging behaviors	[30] [3] [31] [66]

	Devagiri College campus, Calicut, Kerala – urban area – warm humid climatic zone Arunachal Pradesh – Large tracts of tropical, wet evergreen forests and subtropical, temperate and alpine vegetation. Parambikulam Wildlife Sanctuary in Palakkad district of Kerala (76° 35' and 76° 50' East and latitudes 10° 20' and 10° 26' North). Wet tropical climate in protected ecological mountainous zone Pithra village of Simdega district of Jharkhand, Eastern Himalaya zone	Rubber tree plantation (*Hevea brasiliensis*) – BCA Papaya (*Carica papaya*);Mango (*M. indica*). Nutrition and ethnology study. Ethnobiological investigation on wild food traditionally used by the indigenous people as a daily diet – Conservation. Villagers eat fried eggs/broods with salt, chilly, spices and mustard oil, eaten roasted with rice – long term medical preventive usage on many illnesses i.e. scabies, malaria, tooth aches, stomach disorders, blood pressure anomalies Global Food security study (nutrition)	[67] [68] [47] [57] [58]
Bangladesh	Karamjal, Sundarbans, Khulna and Jahangir Nagar University Campus (23º53′N, 90º16′E). Six ecological zones repartition within the Southern-Floodplains: Sundarbans - the largest mangrove forest in the world; Southeastern-Hill Tracts; Northeastern-Hilly Regions; Middle-Plains and Hillocks; Northern-Barind Tracts, red soil and deciduous forest zone; Western-Low Lying Plains, included a positive presence in Lalmai Hill, Cumilla; Faridpur City Jamuna, Meghna (24°07′ N to 25°13′ N latitude and 88°00′ E to 89°10′ E longitude)	Highly degraded sal forest, Jackfruit orchards (*A. heterophyllus*) – Ants surveys checklist Plains, rural residential, forestry, and agricultural areas – ants surveys checklist Unidentified diverse vegetation; Five main areas under the three main rivers of Ganges, Distribution & Phylogeography	[69] [70] [71] [72,73]; [74]
Nepal	Terai, Bhadrapur - foothill (Barne) and middle hill (Kanyam)	Tea garden. Pest surveys identification check list	[75]

Bhutan	Kharbandi Gompa, Phuentsholing (26’85° N, 89’39°E). Pristine natural environment, Forest hills.	Primary forest trees. Not identified - Distribution	[3]

Table 2. Distribution in Indonesia .

Southeast Asia Indonesia	Universitas Negeri Padang (UNP), Air Tawar Barat, Padang, West Sumatra (0°53'49.8"S, 100°21'02.4"E) - lowland area near the coastline	Mangrove *Rhizopora* and *Bruguiera* - *O. smaragdina* collected from a survey check list of ants diversity study – semut rangrang	[76]**
	District North Pariaman, Pariaman city, West Sumatra (0°36’03”S, 100° 06’48”E). Tropical native rainforests, Mangrove forest of Manggung	Tamanu, oil nuts (*Calophyllum inophyllum*) – native species – Ants species diversity check list	[77]**
	Provinces of Java Yogyakarta, Sumatra, Bali, Sulawesi, the eastern part of the Southeast Indonesian Islands	*Leucaena leucocephala* trees offering shades to important Coffee - *Coffea Arabica*, Vanilla – *Vanilla planifolia*; Cocoa – *T. cacao*, Oil palms – *E. guineensis* Jacq. BCA	[78]
		Durian (*Durio zibethinus*) and Citrus (*Citrus aurantiifolia*)/ Distribution	[79]
	Mamburungan village (3016’06.29” N, 117037’12.43” E) on the Tarakan Island in North Kalimantan. Tropical rainforests, agroforestry system	Cacao plantations/ Diversity Surveys study by intensive sampling	[80]
	Bogor Botanical garden (BBG), agroforestry zones, home gardens- Bogor, West Java. Densely populated urban areas	*Eucalyptus* sp., *Acacia mangium*, *Tectona grandis*, *Nephelium lappaceum*, *A. occidentale* and *Shorea* sp. / Biodiversity survey and ants distribution study Dominance of *Oecophylla* in undisturbed forests with positive presence in secondary habitats	[50]

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	Ambon Island Sirimau protected forest 3.6707°; -3.6918° and 128.2394°; 128.2859°. Biogeographycally complex area	Oil palm plantations *Elaeis guineensis* – BCA	[81]
	Gasing village, Tanjung api-api, Banyuasin Regency – South Sumatra. Primary & secondary tropical rainforests	Agarwood, Gaharu (*Aquilaria* sp. *Gyrinops* sp.) – BCA	[82]; [83]
	National Forest Research Institute Kandangan, Barabai, and Balangan Banjarbaru South Kalimantan. Sumbermanjing Wetan Sub-regency, Malang Regency, East Java	Cacao (*Theobroma cacao*) plantations[b] – BCA	[62]
	Banaran, Playen, Gunungkidul, Yogyakarta. Wanagama tropical rainforests	teak wood [c] ,(*Tectona grandis*) – BCA	[27]
	Sulawesi Manado (N 1°33′42.1″ E 124°54′11.6″) – Vast primary & secondary forests – Savanna woodlands	Luxury wood[c] (*Diospyros celebica*) - BCA	[28]
	Nusa Tenggara islands far East- Lembata, Pantar and Atauro. Dominant tropical rainforests and mangroves , coastal strand, savannas, lowlands -	Eucalyptus, Acacia, palm and Ziziphus. Wallacean *Eucalyptus alba* with the endemic *E. urophylla*. Ants diversity check list	[55]

** Tramp invasive species: *Paratrechina longicornis*, *Solenopsis geminata*, and *Tapinoma melanocephalum*. [a]*C. inophyllum*: non edible feedstock as major component for biodiesel production. [b]Large *O. smaragdina* colonies conservation sanctuary. [c]Highly lucrative commercial & popular furniture commodity

Table 3. Distribution in Southeast Asia

Laos	Sivilay Village (18º 15/ N, 102º 27/ E, ca. 200 m alt.), Naxaythong District, located approximately 20 km northwest of Vientiane City	Agroforestry area / mottdaang – Ethnology & global food security	[56]
	Phang Dang Village (18º 14/ N, 103º 01/ E, ca. 500 m alt.), Pak Ngum District, approximately 30 km northeast of Vientiane City	Rare Ants species diversity surveys checklist for Laos	[84]
Cambodia	Kampong Cham Province, Cambodian Rubber Research Institute, (11º55′ N and 105º34′ E) - Forest with 1-2 m high shrubs.	Rubber tree (*H. brasiliensis*) plantations with weeds / angkrang or ongkrong; Ants diversity check litst	[85]
Thailand	Ranong Biosphere Reserve - Andaman Sea coast of southern Thailand (09°50′9ºN, 98°35′E).	Mangrove forest[a] (*Rhizophora mucronata*), *R. apiculata*, *Avicenia* spp., *Aegiceras corniculatum*, *Sonneratia caseolaris* and ground cover provided by *Acanthus ilicifolius* and *Derris trifoliate* / wong mamah – BCA	[86]
	Ban Thaen District of Chaiyaphum Province, Northeast Thailand (16°17′31′′ N 102°14′38′′E)	Pomelo (*Citrus maxima*) plantations – BCA	[87]
Vietnam	Mekong Delta Southern region (10°25′08″N, 106°17′54″E)	Pomelo and orange trees plantations (*Citrus sinensis*) / kiến vàng – BCA study	[88,89]
Timur Leste	Wallacean transitional zone[d] (large tropical native forests): Lautem district far East Timur Leste consisting of Fuiloro plateau, an upland with extensive grassland, sedgeland and Lake Iralalaro, largest freshwater wetland. Mount Legumau is the highest peak at ~1200 m. Nino Konis Santana National Park (half of district) - Mangrove, coastal strand, savannas, lowlands below ~200 m, montane forests in higher-rainfall areas (Paitchau range). On the south coast patches of tropical evergreen forest are found on alluvium behind the beach	Eucalyptus, Acacia, palm and Ziziphus savanna woodlands. Wallacean *Eucalyptus alba* with the endemic *E. urophylla*. Ants diversity check list	[55]
			[90]

Philippines	Cave network, trail-rivers system; Santol Cave, Biak na Bato National Park in Luzon (15°06.475'N, 121°04.539'E). Quezon and Laguna	Cocoa plantations – Ants taxonomy/diversity and BCA Cocoa plantations – Ants taxonomy/diversity and BCA	[91]

. [a]Ecological conservation importance by good maintenance effect. Extensive *Oecophylla* colonies occupation

Table 4. Distribution in Malaysia, Singapore and China

Malaysia	Monoculture of oil palm – Banting Selangor (02°48.15'N, 101°27 .67E) & Tawau, Eastern Sabah (03°22. 54'N, 117°51 .31'E) Primary reserve rainforests & mangrove forests. Tawai Hills Forest Reserve (THFR), the Deramakot Forest Reserve (DFR) and the Sepilok Forest Reserve (SFR), Danum Valley Conservation Area Krau Wildlife reserve forests at Kuala Lompat, Temerloh, Pahang Nature Park, Kuala Selangor (3°17' N, 101° 16'E); Rainforests, Trolak, Perak (3°50'N, 97°52'E)	Oil palm trees (*E. guineensis*), Water guava (*Syzygium aqueum*) / semut kerangga – Ecology & Predation BCA Oil palm trees plantations – Palm fronds – Ants diversity check list Ants check list conservation & species biodiversity Ants species diversity check list Exotic big leaf mahogany timber trees (*Khaya ivorensis*, *Swietenia macrophylla*) – BCA	[13,14] [52] [54] [92] [40,41] d

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	Natural Forest protected Reserve, Forest Research Institute Malaysia (FRIM), (3.2256°N, 101.6260°E)	*Balanocarpus heimii*, *Artocarpus heterophyllus*, and *Dyera costulata* trees	[49]
	Ulu Gombak Field Studies Research Centre (University of Malaya), 20 km North of Kuala Lumpur. Low land rainforests & secondary forests.	Cacao (*T. cacao*) & coconut (*C. nucifera*) plantations	[93]
Singapore	MacRitchie Reservoir at Central Catchment Nature Reserve. Wetland Reserve tropical climate.	2 m height native forests flowers Yellow Saraca, Talan, Bunga Asoka (*Saraca thaipingensis*)	[59]
	Parks, flowering gardens, forest edges, scrubland Pasir Ris – highly populated urban environment	Malabar melastome, Singapore rhododendron, senduduk. Tropical medicinal shrub (*Melastoma malabathricum*) / semut kerangga; *Oecophylla* – Ecology & behaviors: pollinators relation	[94,95]
	Dense urban high-tech city, north, northeast, east, central, and west parts of Singapore	Moth caterpillar, *Homodes bracteigutta*, the crab spider, *Amyciaea lineatipes*, and the jumping spider, *Myrmarachne plataleoides* behaviour study. Fish-tail palm (*Caryota mitis*) – Host plants	[96]
China	Menglun town, National Nature Reserve (largest tropical primitive forest) - Xishuangbanna Dai Autonomous Prefecture of China's southern Yunnan (latitude ranging from 21.15°N to 29.20°N)	Invasion of health care facilities	[53]
	Sihui, Guangzhou, and Huaanin Southern China. Humid sub-tropical to tropical climate.	Primary and secondary forests and rubber plantation habitats/yellow ant – BCA	[97]
	Xishuangbanna Tropical Botanical Garden, Yunnan province (21º55' N, 101º15'E) - tropical season rain forest vegetation types; "Nabanhe River Basin National Nature Reserve in the Autonomous Prefecture" (22°14' N, 100°36' E). Tropical Mountain Rainforest; Xishuangbanna National Natural Park.	Natural habitat: Chinese olive (*Canarium album*). Introduced to Jar orange or sweet orange (*Citrus sinensis*), red-fleshed navel orange (*C. sinensis* "cara cara") mandarin orange & tangerine (*C. reticulata*), lychee (*Litchi chinensis*), Longkong (*Lansium domesticum*), lemon (*C. limon*), pomelo (*C. maxima*) – BCA	[98]
			[95]

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	Protected Area Menglunzi Nature Reserve Chinese Academy of Sciences Xishuangbanna. Botanical Garden (21°55' N, 101°15' E) with a tropical season rain forest vegetation types	Diverse plants: black thorn (*Acacia mearnsii*); antidiarrheal wood tellicherry bark (*Holarrhena antidysenterica*) a medicinal plant for treatment of constipation, colic, and diarrhea; *Oecophylla* – pollinator relation Rubber tree (*H. brasiliensis*), cloud tree or Cowa Mangosteen (*Garcinia cowa*). Ants species diversity check list	[29]

Table 5. Distribution in Australia and Pacific islands

Australia	Queensland, Australia (24.17°S, 151.88°E). Warm climate Northern territory University, Howard Springs Farm and LaBelle Downs Station. Tropical monsoonal area Southeast Darwin (12°40′S, 130°81′E). Tropical monsoonal climate savanna area North Queensland & Northern Territory. Seasonal dry & wet periods under alpine and rainforests area Campus of the James Cook University in Townsville, Cairns (19°19′42″S, 140°45′30″E). Savannah woodlands Charles Darwin University campus in Darwin, Australia (12° 22′13″S, 130° 51′53″E). Tropical climate - distinctive dry and wet seasons	Undefined species - Distribution Cashew nuts (*A. occidentale*) – BCA Mango (*M. indica*) – BCA/IPM Ethnology study on aborigines diet inclusion of *Oecophylla* ants in their menu Unidentified hosts – behaviour Semi-natural eucalyptus savannah-Mating behaviour	[3] [17] [99] [100,101,21] [12] [24]

	Southern frontier of dissemination on the West coast and Yeppoon Qld (23º6'S) on the East coast. Queensland distribution corresponding to 15ºS strictly on the coastal plain only at (16º50'S) the west of Cairns.	Distribution study in Australia highlighting two factors for its limit: minimal temperature 12°C and altitude 500 m	[42]
	Berrimah Farm (12° 52' S, 131° 11' E) and Howard Springs (12° 54' S, 131° 22' E), Darwin Northern Territory	African mahoganies (*Khaya senegalensis*) – BCA	[102]
Solomon Islands	Howard Springs (22 km south-east of Darwin) (12°40'S 130°81'E), Northern Territory	Kensington Pride & Pekaja variety mango orchards – IPM	[103]
	Kukum on the North coast of Guadalcanal.	Coconut plantations – Surveys	

C. inophyllum [104]

3.2. Alien ant species threats – Oecophylla services versus disservices

Some studies highlighted the emergence of tramp ant invasive species (*Anoplolepis gracilipes*, *Tapinoma melanochepalum*, *Tetramorium simillimum*, and *T. bicarinatum),* [52] fast expansion harming indigenous species in by spreading from Indonesia coastline, taking shelter among the mangrove ecosystems [76,77]. As an indigenous species *Oecophylla* ant distribution could be affected in the long term by the invasive yellow crazy ant *A. gracilipes* reputed as a global disruptive ecological factor [105] and *Solenopsis geminata* known to monopolize large resources [106]. Such invasion are more stringent in disturbed native forest converted to agricultural lands or urban areas and if species richness balance was still maintained, as *O. smaragdina* and *A. gracilipes* contribution to beta diversity was highest, the native species eco-system services became weaker [106]. *Oecophylla* keys services are pharmaceuticals-medical, food provision [107], promoting selective pollinators by repulsing the less effective species [108], and nutrient cycle on adsorption directly on host leaves [109,33,110,34]). Despite the important ecosystem services provided by the Asian *Oecophylla* [111], some study did qualify the generalist predator as a pest in large commercial tea plantations of Eastern Nepal based on surveys recording the forager activity of feeding on stems and roots [75]. The pathogenic and lethal *klebsiella* spp. bacteria detected on *Oecophylla* workers guts is reported as a potential infectious risk in urban areas [112]. Repelling of pollinators [38] did not trigger any negative fruit setting impact (Kazuki Tsuji, pers. com) but rather promoted the most efficient pollinators by targeting only the less proficient species [113,96]. The mutualistic relation between weaver ant tended trophobiont honeydew producers sheltered and feeding on plants stems engaging physiological cost to the host plants are rare cases of disservices [40,114]. However in the case of mango orchards in Thailand, the control fail cause *Oecophylla* develop mutualistic association with honeydew producer leafhopper with 125% less profit compare to chemicals treatments: resulting in fruit flowers destruction (no fruit setting), [87].

3.3 Nesting biology of O. smaragdina

O. smaragdina is never subterranean but some nests have been found on the ground under heaps of debris or piles of vegetation [44] in contrast to their usual arboreal nature. Although this new observation did not determine the type of ground nests, it is probably the defensive “barracks” (and less likely brood nests type), inhabited only by major workers [14].

Upon the first emergence of offspring late instar larvae, the gravid queen will gently squeeze the larvae by using them as a shuttle along the end leaves to be spun with whitish silk, eventually constructing the first habitat nest to house future colony workers. The first emerging workers must open the chamber to get off the ground and begin foraging activities in search for food items and new territories [115]. Asian and African weaver ants have an established unique arboreal nests construction by binding living leaves with the sticky white silk (Fig. 2(A-D) of late instar larvae stimulated by major workers [116]. With the sufficient increase in the population of workers, new tasks are systematically organized to expand the new colony, in the form of a complex partnership between workers and larvae, giving one of the best examples of perfection in collective intelligence among ants, a vivid demonstration of their inner sense of eusocial group problem resolution ability going beyond individual engagement [1,117,118].

The task of building nests in tree canopies is complex and requires a great deal of cooperation and coordination between the major workers [119]. *Oecophylla* workers usually demonstrate a high level of synergistic and effective collective action with the main strategy of cost- and energy-saving goals. The task division is articulated as follows: (i) ants literally “pull the leaves together” by adjusting the number of workers needed accordingly from a single ant to a bridge based on the length of the gap to form a chain like a “self-assemblage” [120], (ii) ants holding each other’s petiole with their mandibles, whereas the first ant is firmly attached to the selected leaf to be dragged over; (iii) the last ant of the chain uses its powerful tarsal pads to be strongly nailed to the leaf, (iv) the ants’

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chain on contraction closes the gaps to be supplanted by others holding the placed leaves, (v) another main worker will use the late instar larvae as a shuttle to glue the leaves from one end to the other with whitish silk that completes the job [103]. Both weaver ants species occupying tree canopies exhibit polydomous patterns (multiple nests in a single tree) in various crops or large rainfall tropical forests [1]. Generally, nests are constructed in diverse sizes, shapes, and arrangements, depending on the type of leaves of the occupied tree [1,31]. There is a complex correlation between the nest location on tree canopies with the size or volume of spatial importance, with environmental factors such as the temperature close to the nest and the wind intensity emerging as best predictors of nests arrangement in the trees [31]. Only few studies have been conducted to investigate the occupation patterns in the oil palm plantation, including details of their external nest features for easy detection [13,14]. Another report came from Indonesia in South Sumatra Province, with a survey on height nest collection of *O. smaragdina* to derive and provide insight into the size and composition of the colonies [81]. In the case of oil palm plantations in Malaysia, in which the species shows a particular interest in the habitat selection, the multiplicity of nests in each tree facilitates the detection of the ants - main and barrack nests appearing on the upper and lower fronds of the canopies, respectively, with several nests disposed on a single frond (Fig. 2D) [13,14]. [121] provided an earlier description of the nesting system mechanism as being the feat between the major workers and late instar larvae close cooperation to seal nest construction structure. Weaver ants are among those species that have the largest colonies in the world. For instance, a colony of 151 nests spreading across eight coconut and four clove trees with a surface area of 800 m^2 was observed [122]. Further, *O. smaragdina* has been reported to occupy about 12 diverse crops in tropical areas [123,100]. [40] check list presented a much higher number of plant hosts in Malaysia only. Fig. 2 A exposed *O. smaragdina* major workers adhesive pads giving them a strong attachment by the legs to the leaves smooth surface [124]. The three pairs of legs exhibited an aroleum located at the terminal pretarsus base section providing a strong grip facilitating vertical walking on surface leaves and branches of arboreal habitat [124].

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Figure 2 A-D. A: Asian weaver ants nest construction by binding oil palm leaflets with successive chains of ants bridging to each other's body by using their mandibles and pads (black arrow). B: A freshly constructed nest with sticky white silk to glue leaves (black circle). C: Newly constructed large nest in Borneo Sabah sighted at the top of oil palm canopy. D: multiple nests in a single frond (red circles). Photos credit: Exélis Moïse Pierre.

4. Mating behaviours – life cycle of *O. smaragdina*

4.1 Mating strategy

Although the scientific community has lately responded with a growing interest in researching specific environmental factors and concepts for the potential implementation of the adoption of weaver ants as a potential biological control agent in various commercial crops across Asia and Africa [7,18]; there is a huge gap in the attention given to the mating behavior of *O. smaragdina* and *O. longinoda* with a only few reports available [10,11,12].

Capitalizing on this knowledge is important to understand the systematic breeding of *Oecophylla* which begin with a nuptial flight with the testimony of numerous drone male and female aggregations called swarming However, this swarming process is not well known in Southeast Asia as most reports have been concentrated in temperate zones

[1,125,126]. Little is known about mating behaviors, as well as the latest study on the mechanism in Australia, by acknowledging that the available data are still at a "rudimentary" level [12]. The existence of the worker brood and winged sexual is taking place throughout the year [12]. Updated mating behaviors information described the initiation of aggregation of sexual on nests top, before aerial swarming, occurring during rainy seasons, under sun absence of cloudy days with higher relative humidity significantly correlated to the nuptial flight occurrences at high altitudes for both species [11,12]. However, the report mentioning that copulation is occurring inside the nest [26] was denied by [10,11], while [12] could only hypothesize on the location of probable spots without providing any evidence. The main difference in mating behaviors between Asian [12] and African weaver ants [10,11] demonstrated nuptial flight occurrences during early sunrise and sunset respectively. Study on the mating behavioral chronology is scarce with the necessity to further study the factors triggering the initiation of the process of the swarming in different geographical zones [10,12]. Firstly, to determine the effects of weather conditions and parameters such as rain, wind, humidity level, air pressure, and moon visibility, on the flight pattern. Secondly, to describe the nuptial flight of males and alate virgin queen and where the copulation takes place; either in the air or inside the nest [10,12]. It is also important to identify type of mating system practices by this species; either monoandry or polyandry (several males mating a single queen), including the existence of monogyny or polygyny (multiple egg laying queens per colony). Initially the Asian weaver ants were considered strictly monogynous [103,121]. Previously, the first case of Asian weaver ants pleometrosis (founding of a colony by several queens) was partially documented [127]. However, the authors concluded that pleometrosis was only temporary to increase early incipient colony survival to help shorten the period to attain maturity, hence inferring those aggregations of dealate queens is a strategic orientation [127]. Upon genesis of a viable colony with the difficulty of a monogynous queen solved, this cooperation for obvious ecological benefits ceased, shifting towards an exclusive reproduction by a single founding queen leaving others annihilated. The first emerging workers took the lead to fully support the daily needs of the colony, easing all burden during nest leaf construction [127]. During a study aim at developing major insect pest control, [102] gave the first report of polygyny describing well maintained cooperation among dealate queens in Australian mango orchards up to the maturity stage. Further study by [128] elucidated *O. smaragdina* colony breeding system structure by using microsatellite markers. Little is known on monoandry or polyandry and its correlation to polygyny for this species, hence the necessity to verify discrepancies among previous reports [19,20,115]. Analysis of the genotype workers arrays of colonies from Australia and Indonesia Javanese side demonstrated the existence of frequent polygyny and polyandry occurrences [128].

Vanderplank declared that the copulation act is happening within the nest, with flying males coming to mate with virgin queens [26](1960). Further study, which would extract valuable knowledge on these various important ecological factors, will eventually help to gain more information to enhance the manipulation of newly established colonies in large monocultures.

4.2. Life cycle history

There is a significant lack of research information on the history of the life cycle of *Oecophylla* genus that has been studied for *O. smaragdina* [103,24] and *O. longinoda* [122,26]. Like others ants species, the life cycle history is articulated around four stages consisting of the process of laying eggs, the formation of larvae, pupae and adults emergence [24]. The evaluation of the life cycle history of the genus shows that the colony is active all the time [26,103,24]. In the process of establishing a new colony, once mated, the mother queen of *O. smaragdina* will take refuge among the live leaves of the tree canopies, selecting the most suitable site (based on safety factors) to lay approximately 35 eggs upon shedding her wings (dealation) on a clean flat surface on naturally rolled or soft leaves

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[24]. However, there is a huge difference in the number of eggs laid in the case of *O. longinoda* [26]. The dealate African weaver ant queen is capable of producing hundreds of eggs [129] with an average of over 900 eggs per day [26]. At a mean temperature of 28ºC, it takes about a month (26 days) from the first larvae emergence to attain adult stage [26]. Fig. 3 showed that at 30°C it takes an average 28 days for the Asian weaver ants for emerging "nanitic" workers caste of intermediate size from the first eggs batch [24,115]. A single egg-laying gravid queen after the nuptial flight under "claustral" condition bringing the first consignment of brood to its mature stage called nanitic workers [121]. In the case of *O. smaragdina*, the eggs laying queens are fundamental to incipient and matured colonies [130,131]. Gravid queens are responsible for the earlier maintenance, nurturing and development of workers [24,131]. The initial generation of workers is entirely dependent on the queen food provision [132]. In autonomous colony foundation, the availability of workers is null, hence the queen is left without any helpers for the future colony survival. In such a case, the queen is qualified to be "claustral", inferring that sufficient metabolic resources are available since outside nest foraging activity is impossible [132].

The weaver ant offers certain advantages as an ant model due to diphasic polymorphism [1]. The three female castes: minor workers, major workers, and the queen can be easily identified due to their morphological differences.

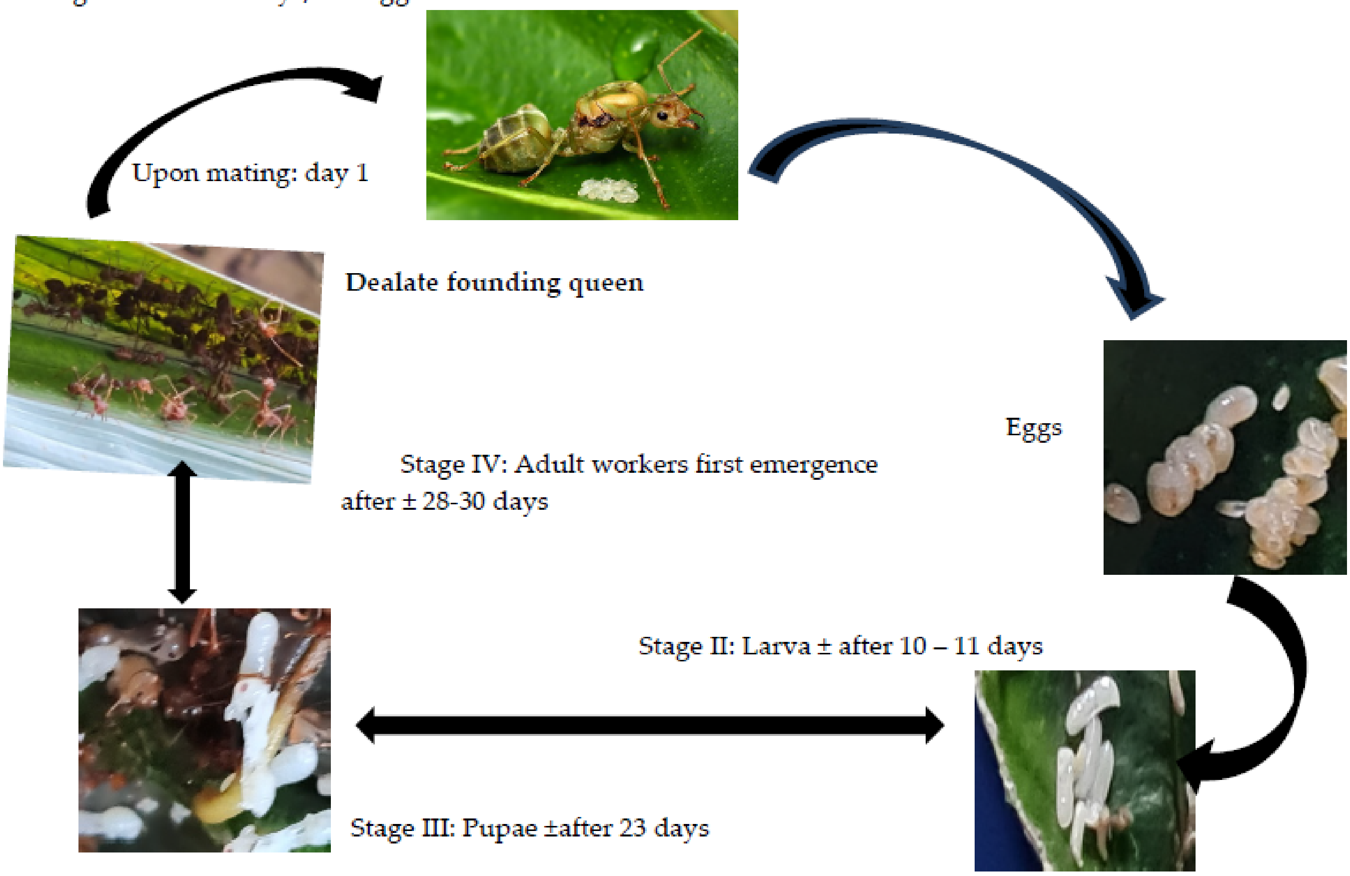

Figure 3. *O. smaragdina* Life cycle chronological stages at 30°C

5. *Oecophylla* colony caste system

The genus *Oecophylla* is organized under a caste system of workers consisting of two sub-castes. The two *Oecophylla* species [133] possess outstanding morphological and behavioral similarities with noticeable body coloration diversity (Fig. 4 A-E), [24]. Mainland Asian workers caste populations are reddish brown [134,13,31,116,119] while the Northern Australian ones possess a green gaster [24], which is similar to the African species

[135,136]. Figs. 3 A-E represented all the variation and organization of caste among *O. smaragdina* found in oil palm plantations [14]. The first sub-castes responsible for foraging and defensive duties are large-sized major workers [137,13]. The second, small-sized minor workers principally nurture the brood inside the nests [115]. Worker ants and reproductive individuals are periodically produced throughout the year [10,12]. Winged, sexual forms are comprised of black and smaller males, whereas virgin queens are green and large. The newly emerged queens are yellow and will turn to green after some time [134,138]. This distinguishes them from the dealate, physogastric, gravid queens, which are reddish-brown and much longer exposing larger abdomens [134,138], (Figs. 4 A-E).

Figure 4 A-E. *O. smaragdina* castes. A: Eggs cluster (yellow circle), larvae (green circle), worker pupae (red circle), major worker (black circle). B: Minor worker (Green arrow), intermediate worker (black arrow), major worker (Red arrow); C: Alate virgin green matured (black circle) and yellow alate immature reproductive newly emerged (yellow circle); D: Black-winged (alate) male (black circle) among major workers (red circle), [139]:.https://www.antwiki.org/wiki/File:Oeco_smaragdina_large_workers_and_males_Peeters.jpg) ; E: Eggs-laid (red circle) from a dealate queen with shed wings (yellow arrow), [140](https://www.inaturalist.org/photos/132294254). Photos credit: Exélis Moïse Pierre (Fig 4 A-C).

Only one report, for Southeast Asia, outlining all growth development stages of *O. smaragdina* from immature (eggs, larvae, pupae) to matured level in Malaysia [134]. The social structure consists of reproductive individuals (dealate queens, alate males, alate females) and non-reproductive ones (major and minor workers), with detailed body size data of all castes [134]. [138] made a brief description of the castes from Laos. Therefore, it is necessary to further establish a comparative study on the species to verify if soil types may affect weaver ant life stages. It is expected that a string of varieties in their color and size with the existence of a potential of novel intermediate workers caste, number of individuals, may emerge upon completion of related study. It is also possible to hypothesize that, if such theory is validated with pertinence, it will intuitively enhance the conviction on probable existing subspecies or even cryptic species within the Asian belt of *O. smaragdina* clusters [19,20]. Hence, the doors for a wider potential research agenda is becoming more apparent and increasing the practical interest of such study at both academic and industrial levels. This is a novelty in the itinerary of ecological and future phylogenetic investigations [141]. Several authors have recently pointed out the importance of a serious revision on the apparent status of the species especially in the aspects of ecology, phylogenetic, and breeding behaviors [19,20,3,4]. *O. smaragdina* is such a resourceful species with yet more potential applications to uncover as even a new biomaterials product could be derived from the natural larval spun silk to form some tough mat "fibroin matrix" with high quality bonded cell [142]. Finally, a study demonstrated the potent insecticidal potential of *Oecophylla* ants crude methanol and n-hexane extracts with a strongly correlated larvicidal effects against the malaria *Anopheles* spp. mosquito vector; adding another environmentally friendly pest disease control tool [143].

6. Conclusion

The scarcity of available literature on the ubiquitous and heavy presence of Asian weaver ants in large commercial monoculture should be addressed to uncover more knowledge that might demonstrated the important contribution of the species in the ecological balance of tropical agroforestry ecosystems. Rare reported disservices with failed fruit setting related to mutualistic relation with honeydew producer trophobiont reminds of the necessity of updated study. There are still some fundamental and important topics which are not being covered and appropriately answered. These include ant-pollinator interaction impact, mating behavior, life cycle history, and breeding systems as monogynous-polygynous in biogeographically different zones. Further investigations on individual caste differentiation among workers are needed to completely document polymorphic matured colonies. The role of these workers as a potential prospect of biological control agent in commercial crops need to be clarified. Without detailed study, the introduction of weaver ants as biological control agents or within an integrated pest management treatment, may pose detrimental effects to local biodiversity. The Asian *Oecophylla* potential predation or interference-repellent factor threat posed to various pollinators is yet to be further verified. This review identified some experimental knowledge that are still considered to be at the elementary stage, hence requiring further study. Important ecological subsistence services to both nature and humans are being offered by the versatile impact of Asian *Oecophylla*. As a provider of organic nutrients for host plants and a highly healthful diet enhancer (nourishing-medicinal), it does combine positive economic implications to food security global concerns and profitable business ventures.

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