

The highly invasive Siam Weed, *Chromolaena odorata* (L.) King and Robinson (Asteraceae), as a seasonal prime nectar source for butterflies (Lepidoptera: Papilionoidea) and other insects (Insecta: Lepidoptera, Hymenoptera, Coleoptera) in West Africa

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Abstract: During mass-blooming in the dry season, the highly invasive Siam Weed, *Chromolaena odorata*, appears to be a prime nectar source for butterflies and a range of diurnal moths and other insects in West Africa. About 10 % of the West African butterfly fauna were recorded visiting *C. odorata* flowers between Sierra Leone and Western Cameroon as a result of opportunistic observations between 2010 and 2021. Predators on flower-visiting insects, such as crab-spiders and Flower Mantises, also seem to have become adapted to the newly available food-source. These records indicate that beyond the well-known adverse effects of *C. odorata* invasion to regeneration of natural vegetation on disturbed ground and the exposure of natural rainforest habitats to wildfires because of the plant's susceptibility to fire, the diet shift of a considerable proportion of pollinators could imply further threats to biodiversity, such as reducing the reproductive rate of forest plants previously pollinated by butterflies. Specific studies further targeting the subject are urgently needed.

Key words: *Chromolaena odorata*, *Eupatorium odoratum*, Asteraceae, Compositae, biological invasion, nectaring, pollination, predation, biodiversity, Lepidoptera, Rhopalocera, Heterocera, Mantidae, Thomisidae.

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INTRODUCTION

Siam Weed (Jack-in-the-bush in its native America), *Chromolaena odorata* (L.) King and Robinson, formerly known as *Eupatorium odoratum* L., is a perennial plant in the Asteraceae family and is among the worst invasive weeds in the World, seriously affecting agriculture and biodiversity in the tropics and subtropics of the Old World (Zachariades *et al.*, 2009). In Sub-Saharan Africa it is known to have first been introduced accidentally to Nigeria in the 1930s from its original subtropical-tropical American distribution, probably with seeds of the cultivated South American tree species, *Gmelina arborea* Roxb. (Zachariades *et al.*, 2009). Deliberate introduction was documented in Ivory Coast as a potential shading plant in coffee and oil palm plantations in the 1950s (de Rouw, 1991). From these initial centres of occurrence, the species began to spread aggressively across the West Coast of Africa, and is now widely distributed across the Guineo-Congolian forest zone between southern Senegal and western Uganda (CABI, 2021).

C. odorata establishes most easily on disturbed ground in originally rainforest-covered areas, such as road verges, clearings and farms, where the pappus-aided seeds can quickly germinate. The plant can bloom within a year (Fig. 1), producing tens of thousands of seeds, and could

invade vast areas, creating impenetrable thickets within a few generations (Fig. 2). In Ivory Coast, *C. odorata* has contributed to the country's deforestation, as its rapid invasion has extended the time of regeneration of fallow vegetation in the slash and burn agriculture regime. The cost of continuous weeding and application of agrochemicals also exceeded the profit expected in heavily infested agricultural land. As a result, new rainforest areas were cleared (de Rouw, 1991), where the revenue from the felled timber trees and charcoal burning compensated the farmer's loss.

In West Africa, as in other areas of its distribution, *C. odorata* flowers almost exclusively during the dry season (CABI, 2021), starting from the end of October and continuing until late February or early March, depending on local weather conditions. Mass flowering was observed from mid-November until the end of January when conditions become too dry to maintain the continuous development of flowering shoots, but locally more humid conditions can extend flowering (Sáfián, pers. obs.). It was previously observed that *C. odorata* mass flowering attracts a wide range of insects, with a vast majority of them being butterflies, in tropical Asia (Shihan & Kabir, 2015; Rathnayake & Wijetunga, 2016; Hasan *et al.*, 2018). The flowering plant was recorded as a major attractor of insects, including a high proportion of Lepidoptera (hawk-moths and butterflies), Hymenoptera (bees and wasps) and Diptera (Syrphidae) by (Lakshmi *et al.*, 2011) in India. They highlighted that *C. odorata* is psychophilous and pollination is highly dependent on the visiting butterfly community.

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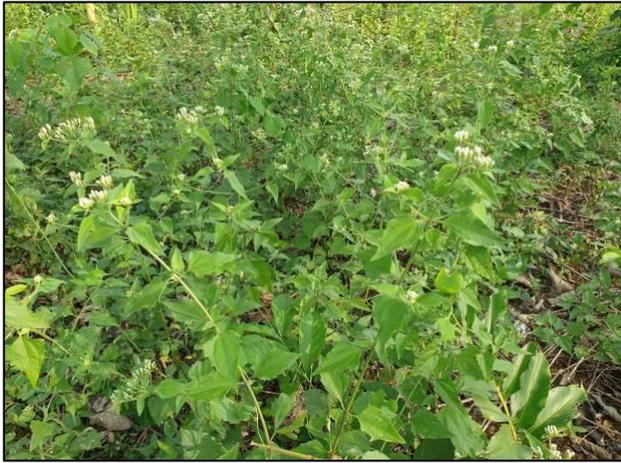


Figure 1 – First year *C. odorata* plants before full bloom.



Figure 2 – Impenetrable *C. odorata* thickets are quickly established along disturbed forest edges and after farming in forest areas, suppressing the regeneration of natural vegetation and increasing the risk of wildfires, but at the same time they provide nectar-source for millions of insects.

The author did not find specific references for the nectaring or pollen-feeding visitors and potential pollinators of *C. odorata* on the African continent except the few butterfly species mentioned in Larsen (2005), despite the plants significance in agriculture and biodiversity conservation. For this reason, he started recording butterflies nectaring on *C. odorata* opportunistically in 2010 in the Putu Range, Liberia. The observations became more frequent in 2013, with further localities involved, after he realized how regularly the *C. odorata* flowers are visited by butterflies, often in large numbers.

This paper highlights these West African records in the hope that they will draw attention to invasion ecology, using *Chromolaena odorata* as one of the model plants in tropical Africa.

MATERIALS AND METHODS

The abbreviations of localities (from west to east), and literature source (wherever applicable) are as follows. The

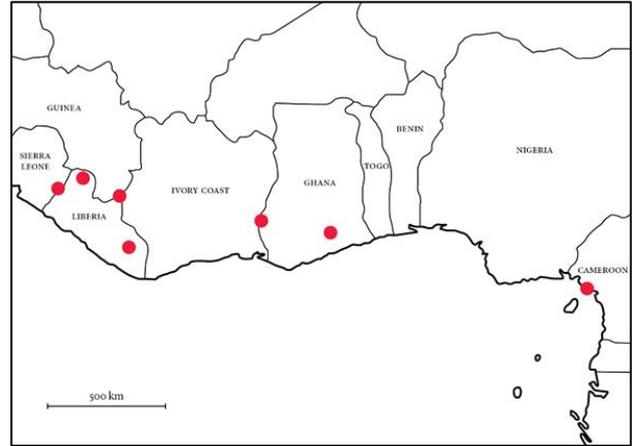


Figure 3 – Localities where observations of butterflies nectaring on *C. odorata* flowers in West Africa were made.

distribution of the localities of observations are illustrated in Fig. 3.

GOL – Gola Rainforest National Park (ex Gola Forest Reserves), Sierra Leone

WOL – Wologizi Mountains, Liberia

NIM – Nimba Mountains, Liberia

KPA – Kpatawee Waterfalls, Liberia

PUT – Putu Range, Liberia

BIA – Bia National Park, Ghana (Larsen 2005)

ATE – Atewa Range, Ghana (Larsen 2005)

BIM – Bimbia-Bonadikombo Community Forest, Cameroon

LAR – Torben Larsen's (2005) observations without locality given

Butterfly habitats in the Gola Rainforest National Park, Sierra Leone are described in Belcastro & Larsen (2006) and Sáfián (2010, 2012), habitats in the Wologizi Mountains are described in Sáfián *et al.*, 2020, while those in the Nimba Mountains in Liberia are described in Sáfián (2014). Habitats in the Bia National Park are discussed in Larsen (2006) and those in the Atewa Range in McCullogh *et al.* (2007). The habitats in Bimbia-Bonadikombo Community Forest in Cameroon are extensively discussed in Ferenc *et al.* (2018).

The order of genera follows Williams (2015), except where further revisions have established new generic names (e.g. *Torbenlarsenia* Kemal & Koçak, 2020) (Kemal & Koçak, 2020). The names at specific and subspecific level are based on Larsen (2005) but subsequent updates (e.g. Henning & Williams, 2010, 2020; Larsen 2012) and new descriptions (Sáfián *et al.*, 2020) are followed.

Taxa that could not be identified to species level due to the similarity to other species are listed as sp., while the identical *Telchinia alciops* (Hewitson, 1852) and *T. aurivillii aurivillii* (Staudinger, 1896), which can only be separated on the basis of the male genitalia in West Africa (Larsen 2005), are both listed.

RESULTS

Butterflies observed nectaring on *C. odorata*

Altogether 153 butterfly species, in five families and 67 genera, were recorded nectaring on *C. odorata*, of which 147 were captured or observed by the author as part of the current study. Additional records were published in Larsen (2005), in most cases using the name *Eupatoria odoratum*, a synonym of *Chromolaena odorata*.

PAPILIONIDAE

Graphium polices polices (Cramer, [1775]) – NIM
Graphium antheus (Cramer, [1779]) – NIM
Papilio demodocus Esper, [1798] – KPA
Papilio phorcas phorcas Cramer, [1775] – NIM
Papilio nireus nireus Linnaeus, 1758 – BIM
Papilio cynorta Fabricius, 1793 – NIM

HESPERIIDAE

Coeliades chalybe chalybe (Westwood, [1852]) – NIM
Coeliades forestan forestan (Stoll, [1782]) – KPA, NIM
Coeliades pistratus (Fabricius, 1793) – NIM
Coeliades hanno (Plötz, 1879) – NIM
Tagiades flesus (Fabricius, 1781) – WOL, KPA, NIM, PUT, BIM (Fig. 4)
Eagris tetrastigma lomana Belcastro & Sáfián, 2020 – NIM
Sarangesa majorella (Mabille, 1891) – KPA
Sarangesa thecla thecla (Plötz, 1879) – NIM
Sarangesa bouvieri (Mabille, 1877) – NIM
Abantis tanobia Collins & Larsen, 2005 – NIM
Prosopalpus saga Evans, 1937 – NIM
Gorgyra aburae (Plötz, 1879) – KPA
Ceratrachia phocion phocion (Fabricius, 1781) – NIM
Ceraticula semilutea (Mabille, 1891) – NIM
Xanthodisca rega (Mabille, 1889) – NIM
Parosmodes lentiginosa (Holland, 1896) – NIM
Osphantes ogowena ogowena (Mabille, 1891) – PUT
Paracleros sp. – NIM
Acleros ploetzi Mabille, 1889 – NIM
Acleros mackeenii olaus (Plötz, 1884) – NIM
Semalea pulvina (Plötz, 1879) – NIM
Semalea arela (Mabille, 1891) – NIM
Meza elba (Evans, 1937) – NIM
Meza mabillei (Holland, 1893) – NIM
Meza cybeutes volta Miller, 1971 – NIM
Andronymus caesar caesar (Fabricius, 1793) – KPA, NIM
Andronymus hero Evans, 1937 – NIM
Andronymus evander (Mabille, 1890) – KPA, NIM
Caenides hidaroides Aurivillius, 1896 – NIM
Caenides dacena (Hewitson, 1876) – NIM
Monza alberti (Holland, 1896) – KPA
Monza cretacea (Snellen, 1872) – NIM
Mephinyet tarace (Mabille, 1891) – NIM
Fresna netopha (Hewitson, 1878) – NIM
Platylesches galesa (Hewitson, 1877) – NIM
Platylesches rossii Belcastro, 1986 – NIM
Platylesches batangae group – NIM
Platylesches picanini (Holland, 1894) – NIM, PUT, BIA
Borbo fatuellus fatuellus (Hopffer, 1855) – NIM
Torbenlarsenia perobscura (Druce, 1912) – NIM
Torbenlarsenia gemella (Mabille, 1884) – NIM
Afrogegenes sp. – NIM

NYMPHALIDAE

DANAINAE

Danaus chrysippus (Linnaeus, 1758) – WOL, KPA, NIM (Fig. 5)
Amauris niavius niavius (Linnaeus, 1758) – NIM, BIM
Amauris tartarea tartarea Mabille, 1876 – NIM
Amauris damocles damocles (Fabricius, 1793) – NIM

SATYRIDAE

Ypthima doleta Kirby, 1880 – NIM

NYMPHALINAE

Vanessa cardui (Linnaeus, 1758) – NIM
Antanartia delius delius (Drury, 1782) – WOL
Precis octavia octavia (Cramer, 1777) – WOL
Precis pelarga (Fabricius, 1775) – BIM
Precis sinuata sinuata Plötz, 1880 – NIM
Hypolimnas misippus (Linnaeus, 1764) – WOL, KPA, NIM
Hypolimnas salmactis salmactis (Drury, 1773) – BIM
Protogoniomorpha cytora (Doubleday, [1847]) – NIM
Protogoniomorpha parhassus (Drury, 1782) – NIM
Junonia oenone oenone (Linnaeus, 1758) – KPA, NIM
Junonia terea terea (Drury, 1773) – KPA, NIM
Catacroptera cloanthe ligata Rothschild & Jordan, 1903 – NIM

CYRESTINAE

Cyrestis camillus (Fabricius, 1781) – NIM, BIM

HELICONIINAE

Acraea camaena (Drury, 1773) – KPA, NIM
Acraea endoscota Le Doux, 1928 – KPA, NIM
Acraea eugenia Karsch, 1893 – BIM
Acraea quirina (Fabricius, 1781) – WOL, KPA, NIM, BIM (Fig. 6)
Acraea abdera eginopsis Aurivillius, [1899] – PUT
Acraea egina egina (Cramer, [1775]) – WOL, KPA, NIM, BIM
Acraea pseudegina Westwood, [1852] – BIM
Acraea kraka Aurivillius, 1893 – PUT (Fig. 7)
Acraea rogersi Hewitson, 1873 – NIM, BIM
Acraea consanguinea consanguinea (Aurivillius, 1893) – BIM
Acraea epaea epaea (Cramer, [1779]) – NIM, BIM
Acraea macaria (Fabricius, 1793) – NIM
Acraea vestalis vestalis Felder & Felder, [1865] – NIM (Fig. 8)
Telchinia alciope (Hewitson, [1852]) /
T. aurivillii aurivillii (Staudinger, 1896) – NIM, PUT, BIM
Telchinia bonasia (Fabricius, 1775) – NIM
Telchinia circeis (Drury, 1782) – WOL, NIM
Telchinia encedana (Pierre, 1976) – KPA
Telchinia jodutta jodutta (Fabricius, 1793) – WOL
Telchinia lycoa (Godart, [1819]) – NIM, PUT, BIM
Telchinia pharsalus (Ward, 1871) – NIM, BIM
Telchinia polis (Pierre, 1999) – PUT, BIM
Telchinia serena (Fabricius, 1775) – KPA
Telchinia vesperalis (Grose-Smith, 1890) – PUT
Telchinia oberthueri (Butler, 1895) – BIM
Telchinia orestia (Hewitson, 1874) – BIM
Telchinia peneleos peneleos (Ward, 1871) – NIM, ATE, BIM
Telchinia penelope derubescens (Eltringham, 1912) – LAR
Telchinia perenna perenna (Doubleday, [1847]) – NIM, BIM

Lachnoptera anticlia (Hübner, [1819]) – KPA, NIM
Phalanta eurytis eurytis (Doubleday, [1847]) – NIM

LIMENITINAE (LIMENITIDINAE)

Cymothoe egesta (Cramer, [1775]) – NIM
Cymothoe sangaris sangaris (Godart, [1824]) – NIM
Pseudacraea semire (Cramer, [1779]) – NIM
Neptis nemetes nemetes Hewitson, [1868] – KPA, NIM
Neptis saclava marpessa Hopffer, 1855 – BIM
Neptis serena serena Overlaet, 1955 – WOL, NIM
Neptis agouale Pierre-Baltus, 1978 – NIM

PIERIDAE

Catopsilia florella (Fabricius, 1775) – WOL, KPA, NIM
Eurema senegalensis (Boisduval, 1836) – NIM
Eurema hecabe solifera (Butler, 1875) – KPA, NIM, BIM
Nepheronia argia argia (Fabricius, 1775) – KPA, NIM
Nepheronia thalassina thalassina (Boisduval, 1836) – KPA, NIM
Belenois calypso calypso (Drury, 1773) – KPA, NIM, BIM
Appias sylvia sylvia (Fabricius, 1775) – NIM
Appias perlucens (Butler, 1898) – BIM
Appias sabina sabina (Felder & Felder, [1865]) – NIM
Leptosia alcesta alcesta (Stoll, [1782]) – NIM
Mylothris chloris chloris (Fabricius, 1775) – NIM, BIM
Mylothris dimidiata Aurivillius, 1898 – NIM
Mylothris sulphurea sulphurea Aurivillius, 1895 – BIM
Mylothris poppea (Cramer, [1777]) – NIM
Mylothris rhodope (Fabricius, 1775) – NIM
Mylothris schumanni schumanni Suffert, 1904 – BIM

LYCAENIDAE

APHNAEINAE

Aphnaeus orcas (Drury, 1782) – NIM
Axiocerses harpax harpax (Fabricius, 1775) – KPA, NIM
Cigaritis crustaria (Holland, 1890) – BIM
Cigaritis iza (Hewitson, [1865]) – GOL, NIM

POLYOMMATINAE

Anthene larydas (Cramer, [1780]) – KPA, NIM, BIM
Anthene sylvanus (Drury, 1773) – BIM
Anthene irumu (Stempffer, 1948) – NIM
Anthene princeps (Butler, 1876) – NIM (Fig. 9)
Anthene amarah amarah (Guérin-Méneville, 1849) – NIM
Neurellipes lusones (Hewitson, 1874) – NIM
Neurellipes juba (Fabricius, 1787) – NIM
Neurellipes lysicles lysicles (Hewitson, 1874) – BIM
Triclema rufoplagata rufoplagata Bethune-Baker, 1910 – KPA
Triclema lamias lamias (Hewitson, [1878]) – NIM
Cupidesthes jacksoni Stempffer, 1969 – BIA
Lampides boeticus (Linnaeus, 1767) – KPA
Leptotes pirithous pirithous (Linnaeus, 1767) – NIM, BIM
Tuxentius carana kontu (Karsch, 1893) – NIM
Eicochrysops hippocrates (Fabricius, 1793) – NIM
Azanus isis (Drury, 1773) – KPA, NIM

THECLINAE (Fig. 10)

Hypolycaena philippus philippus (Fabricius, 1793) – NIM
Hypolycaea liara liara Druce, 1890 – NIM
Hypolycaena lebona-group – NIM, BIM
Hypolycaena antifaunus antifaunus (Westwood, [1851]) – NIM

Deudorix lorisona lorisona (Hewitson, 1862) – NIM, LAR

Deudorix kayonza Stempffer, 1956 – NIM, BIA
Deudorix dinomenes diomedes Jackson, 1966 – BIA
Pilodeudorix cameroni cameroni (Plötz, 1880) – BIA
Pilodeudorix diyllus diyllus (Hewitson, [1878]) – BIA
Pilodeudorix caerulea (Druce, 1890) – LAR
Pilodeudorix leonina (Bethune-Baker, 1904) – NIM
Pilodeudorix virgata (Druce, 1891) – KPA
Pilodeudorix kiellandi (Congdon & Collins, 1998) – NIM
Pilodeudorix violetta (Aurivillius, 1897) – NIM, LAR

The butterflies observed nectaring on *C. odorata* represent the five major African families, Papilionidae, Hesperidae, Nymphalidae, Pieridae and Lycaenidae, excluding only Riodinidae, members of which are generally very scarce in West Africa and tend to stay inside closed canopy forest in good condition (Larsen 2005). Although all species are known to be nectar-feeders, members of Papilionidae represent only 4 % of all recorded species, as the family is rather species-poor in West Africa. Pieridae are also generally nectar-feeders and tend to seek food in open areas and forest edges rather than in the darker forest interior (except for a few species of *Leptosia* and the unique *Pseudopontia*) (Larsen 2005), but the family is not particularly species-rich in West Africa with only 11 % of the recorded species belonging to Pieridae. Many of them are common, with good dispersal abilities, and with tolerance for habitat degradation. Lycaenidae make up 22 % of all species recorded, dominated by the subfamilies Polyommatainae and Theclinae and are only exceeded by Hesperidae, representing 27 % and Nymphalidae 36 % of all species recorded.

Moths observed nectaring on *C. odorata*

Only diurnal moths were recorded during the observations, but nocturnal groups are also expected to visit the flowers. Most often two common species of Synthomiini were observed nectaring on *C. odorata*; a species near *Amata alicia* (Butler, 1876)/*A. francisa* (Butler, 1876) (Fig. 11) and *Euchromia folletii* (Guérin-Méneville, 1832) (= *formosa* (Boisduval, 1833)) (Fig. 12). A number of Crambidae also frequently visit *C. odorata* flowers, including *Bocchoris inspersalis* (Zeller, 1852) and *Phostria hesusalis* (Walker, 1859) as observed in the Nimba Mountains. They are normally nocturnal and are attracted to artificial light (Poltavsky *et al.*, 2019), but it seems that the availability of the food-source may also influence their general feeding habits. Day-flying Hyblaeidae also feed on the nectar of *C. odorata* as observed on a few occasions (Fig. 13). A single clearwing specimen in the tribe Synanthedonini (Sesiidae, Sesiinae) was collected on *C. odorata* in January 2001 by the author in Bia National Park, Ghana and a single pterophorid was observed on the flowers at Kpatawee Waterfalls, Liberia. Other micromoths were also seen on the flowers during the day, but only occasionally.

Other insects and predators observed on *C. odorata*

C. odorata flowers attract an incredible variety of nectar/sugar/pollen-feeding insects, often also a great number of individuals. Of Hymenoptera, Africanized Honey Bee (*Apis mellifera scutellata*) workers are among

the most frequent visitors (Fig. 14), but various groups of solitary bees and other wild bees (Apoidea) are also attracted. However, passing Carpenter Bees (Xylocopinae) seem to largely avoid *C. odorata*. Several wasp (Vespidae) species were observed feeding on the flowers (Fig. 15). Observations on Diptera were relatively few and were restricted to species of Hoverflies (Syrphidae). Of beetles (Coleoptera), members of Scarabaeidae: Cetoniinae, were the most frequent visitors, such as *Pachnoda cordata obsoleta* Schaum, 1844 and *Oxythyrea (Stichothyrea) guttifera* (Afzelius, 1817) (Figs 16–17).

Predators also seem to adapt very quickly to the newly established rich food source. Visiting insects are often caught by crab-spiders (Araneae, Thomisidae) (Fig. 18), and species of African Flower Mantis (*Pseudocreobotra* spp.) regularly hide among *C. odorata* flowerheads, waiting for prey (Fig. 19).

DISCUSSION

Although butterflies regularly visit flowers of *C. odorata* in West Africa this was previously only noted by Larsen (2005). However, recent opportunistic observations proved that the number of butterfly species utilising the flowers as a nectar source is outstandingly high. Almost 10% of the West African butterfly fauna was recorded nectaring on *C. odorata* flowers and systematic data collection would most probably reveal significantly higher numbers of butterflies utilising the plant. No other flowering plant is known to attract such a large number of nectar-feeding butterflies in West Africa or elsewhere in Sub-Saharan Africa.

Predictably, many open and disturbed habitat species were recorded, as the densest *C. odorata* stands are generally found in fallow farmlands and cleared forest areas, attracting species from the immediate vicinity (e.g. *Papilio demodocus*, *Coeliades forestan*, *Danaus chrysippus*, *Hypolimnas misippus*, *Acraea egina*, *Leptotes* sp.). However, a wide range of strictly forest-dwelling species were also recorded (such as members of the genera *Fresna*, *Meza*, *Andronymus*, *Mylothris* and most species of *Hypolycaena*). A few species observed on the flowers are very rare or are canopy-dwellers, seldom seen at ground level (e.g. *Abantis tanobia*, *Deudorix kayonza*, *Pilodeudorix kiellandi*). Based on the observations forest butterflies are usually attracted to the flowers only, when the *Chromolaena* bushes have penetrated the forest habitat along roads, or they have invaded natural clearings. The majority of them visited the flowers in the early morning between 07.30–09.30, while they were absent during the warmest hours. Some reappear late in the afternoon, after 16.00. Although recording was not systematic, forest butterflies seem to prefer bushes in semi-shaded forest edges and this could be explained by the slower evaporation of water from the nectar in flowers less exposed to the sun but forest species would also naturally avoid feeding on plants in open areas.

Only a few studies on butterflies nectaring on *C. odorata* flowers are available for comparison, and most of them report general observations on the nectaring and pollination by butterflies. A single species, *Eumaeus atala* (Poey, 1832) (Lycaenidae, Thenclinae), was reported

nectaring on *C. odorata* within its native range in Florida, USA (Koi, 2008). Nacua *et al.* (2014) recorded butterfly species from all major families nectaring on *C. odorata* during their study in the Philippines, including the Satyrinae and Libytheinae subfamilies of Nymphalidae and also Riodinidae. Members of the latter two groups were not observed in West Africa (Fig. 20), while records of Satyrinae are limited to a single species *Ypthima doleta*, which is not surprising as most Afrotropical satyrines (Mycalesini) are frugivorous and they generally avoid flowers (Larsen 2005). Even from a nonrepresentative sample it is very clear that Acraeini (Nymphalidae, Heliconiinae) are highly over-represented in the observations with 28 species, and all four currently recognised West African genera of Heliconiinae were observed nectaring on *C. odorata* flowers. The over-representation of members of *Anthene sensu* Libert (2010), in the subfamily Polyommatainae, and the tribe Deudorigiini (genera *Deudorix* and *Pilodeudorix*) in the subfamily Theclinae of Lycaenidae is outstanding. They each make up 6 % of all recorded species. *Anthene* were attracted to the flowers throughout the day, while *Deudorix* were observed exclusively in the early morning hours and *Pilodeudorix* later in the afternoon, after 15.00–16.00.

In general, the representation of butterfly families is more even in the West African observations compared to those in India. Lakshmi *et al.* (2011) recorded 61 % of all butterfly species visiting *C. odorata* flowers to be nymphalids, followed by papilionids (11 %), while lycaenids and hesperiids represented only 8 % and 3 % of all recorded species, respectively. Slightly over one-third of all butterfly species belong to Nymphalidae in the West African observations and both Hesperidae and Lycaenidae constitute significant proportions of the sample, with 27 % and 22 %, respectively (Fig. 20). One of the possible explanations is that the observations in the present study were not restricted to the generally recognised active hours and many species observed actually fed on *C. odorata* only very early in the morning and during the late afternoon hours.

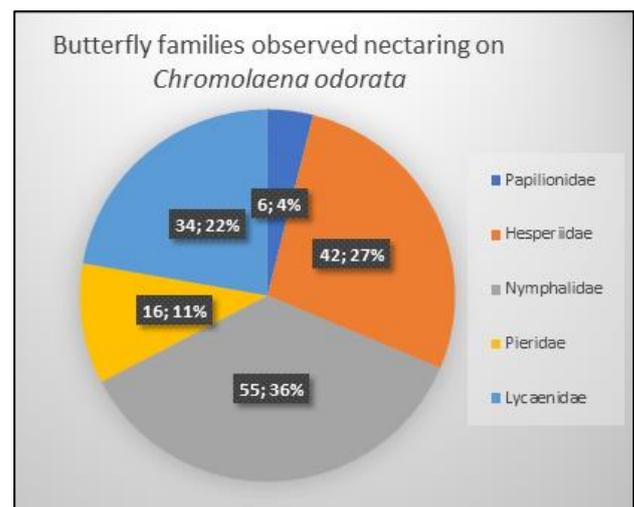


Figure 20 – Butterflies observed nectaring on *C. odorata* by family. The values show the number of species observed and their percentage in the sample.

Implications for conservation

The rapid dispersal of a newly-appearing abundant food source for nectar-feeding butterflies and other insects in forest ecosystems, and the obvious distraction of the pollinator organisms from their original nectar-plant(s) imply further consequences. Although almost no case studies are available on pollinator organisms in connection with *C. odorata*, in a single case the reproductive success of a native forest tree *Dipterocarpus obtusifolius* Teijsm. ex Miq. was adversely affected by alteration of foraging behaviour of butterflies, shifting butterfly activities from the canopy to the understorey as detected in Thailand by Ghazoul (2004). As nectar sources in the West African rainforest understorey is generally sparsely distributed, and forest interior butterflies probably have to invest considerable energy in foraging, the availability of alternative nectar sources along the forest edges could cause a shift of foraging activity towards *Chromolaena*-infested forest edges, particularly in some groups of Hesperiiidae, which are not normally found outside of deep forest (*Meza elba*, *M. mabillei*, *Caenides hidaroides*), and also vertically, since many Acraeini attracted to *C. odorata* flowers would otherwise feed on and pollinate climbers, creepers and forest trees, which produce flowers only in the higher strata of the rainforest (Sáfián pers. obs.). In forested areas in Singapore diet shift reached up to 43% of feeding observations towards non-native flowers (Jain *et al.*, 2016) and such a significant shift of foraging activity could also adversely affect pollination success of native plants in *Chromolaena* infested West African forest areas.

Although studies targeting pollination of *C. odorata* in Africa are completely lacking, Lakshmi *et al.* (2011) invariably found *C. odorata* pollen grains on butterfly probosces across their sample, proving pollen transfer between, and thus successful pollination of, *C. odorata* flowers during foraging. Considering the large number of nectar-feeding visitors observed in West Africa, butterflies and other frequent visitors could also contribute to the high reproduction success of *C. odorata*, and therefore to the success of biological invasion of vast areas in the Afrotropics. This would suppress natural vegetation and prevent or extend the time taken for forest regeneration in abandoned farmlands. It may also lead to further degradation of forest habitats by leading wildfires into the degraded forest interior. In contrast, studies on breeding systems of alien invasive plants in South Africa indicated that *C. odorata*'s reproduction strategy includes apomixis and thus the uniparental breeding system contributed to the success of the species to become one of the most successful colonisers in the forest zone of Sub-Saharan Africa (Rambuda & Johnson 2004).

Some butterfly species would certainly benefit from the availability of the rich nectar source provided by *C. odorata* plants but the population densities of rarer species are normally regulated by multiple other factors, such as occurrence and abundance of larval foodplant, habitat structure, microclimate and altitude, while the availability of an additional nectar source would have negligible positive effects on their populations.

Specific studies are urgently needed to understand the

influence of *Chromolaena* invasion in relation to butterflies and other pollinating insects and their natural nectar-plants in West Africa.

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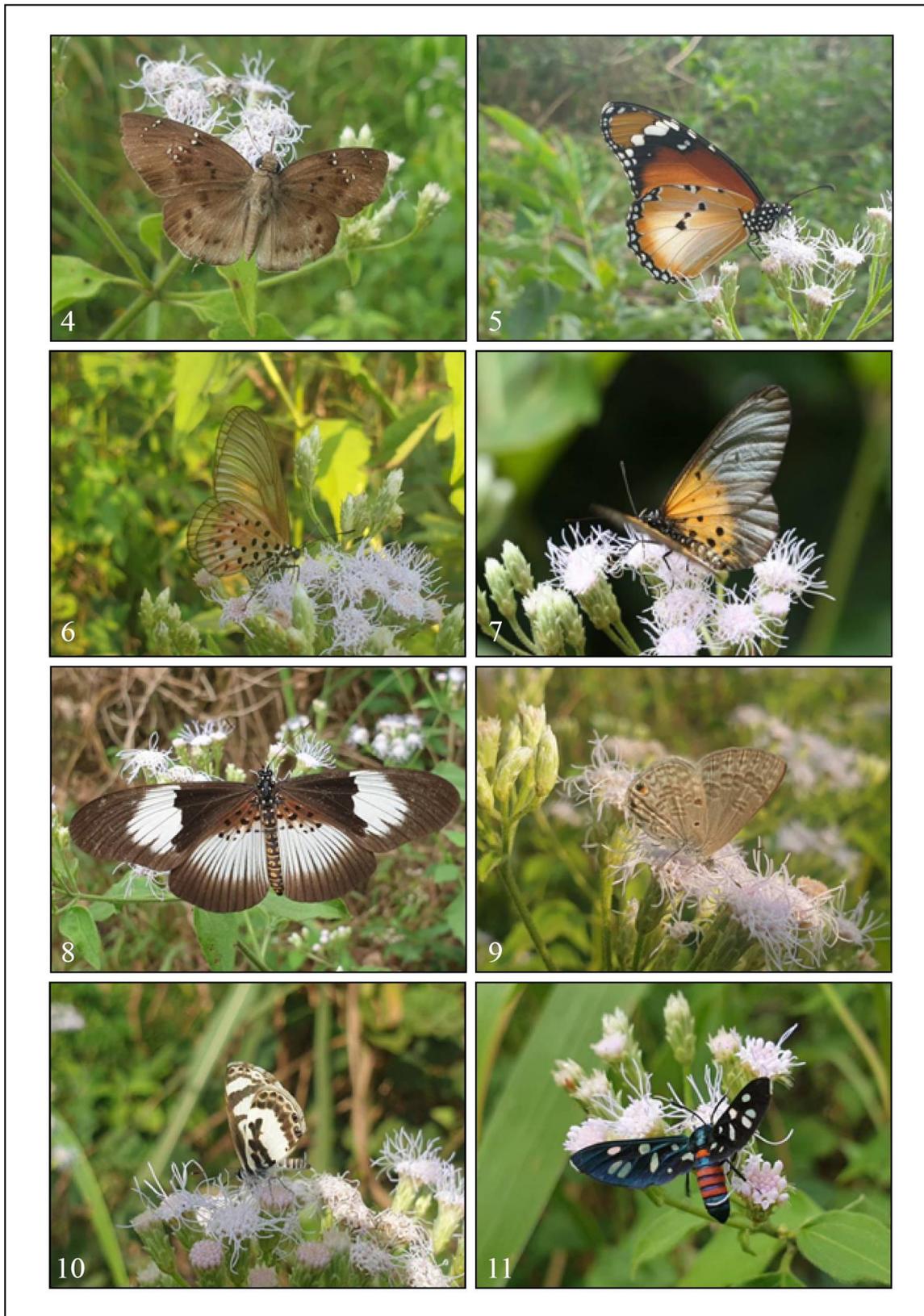


Figure 4 – Female of *Tagiades flesus*, a common forest butterfly nectaring on *C. odorata*.

Figure 5 – Male of *Danaus chrysippus*, a cosmopolita, ubiquitous species nectaring on *C. odorata*.

Figure 6 – Male of *Acraea quirina*, a common forest butterfly is nectaring on *C. odorata*.

Figure 7 – Male of *Acraea kraka* nectaring on *C. odorata*. In West Africa west of the Dahomey it is an upland specialist, occurring only above 700 m altitude in isolated colonies between Ghana and Liberia. In the Putu Range in Liberia, mining exploration opened roads in the unique upland forest, causing invasion of *C. odorata*.

Figure 8 – *Acraea vestalis vestalis* female is a rare visitor of *C. odorata*.

Figure 9 – Female of *Anthene princeps*, a common savannah butterfly nectaring on *C. odorata*.

Figure 10 – Male of *Azanus isis*, a common forest butterfly is nectaring on *C. odorata*.

Figure 11 – Syntomina species near *Amata alicia* (Butler, 1876)/*A. francisa* (Butler, 1876) (Erebidae, Arctiinae), a common visitor on *C. odorata* flowers.

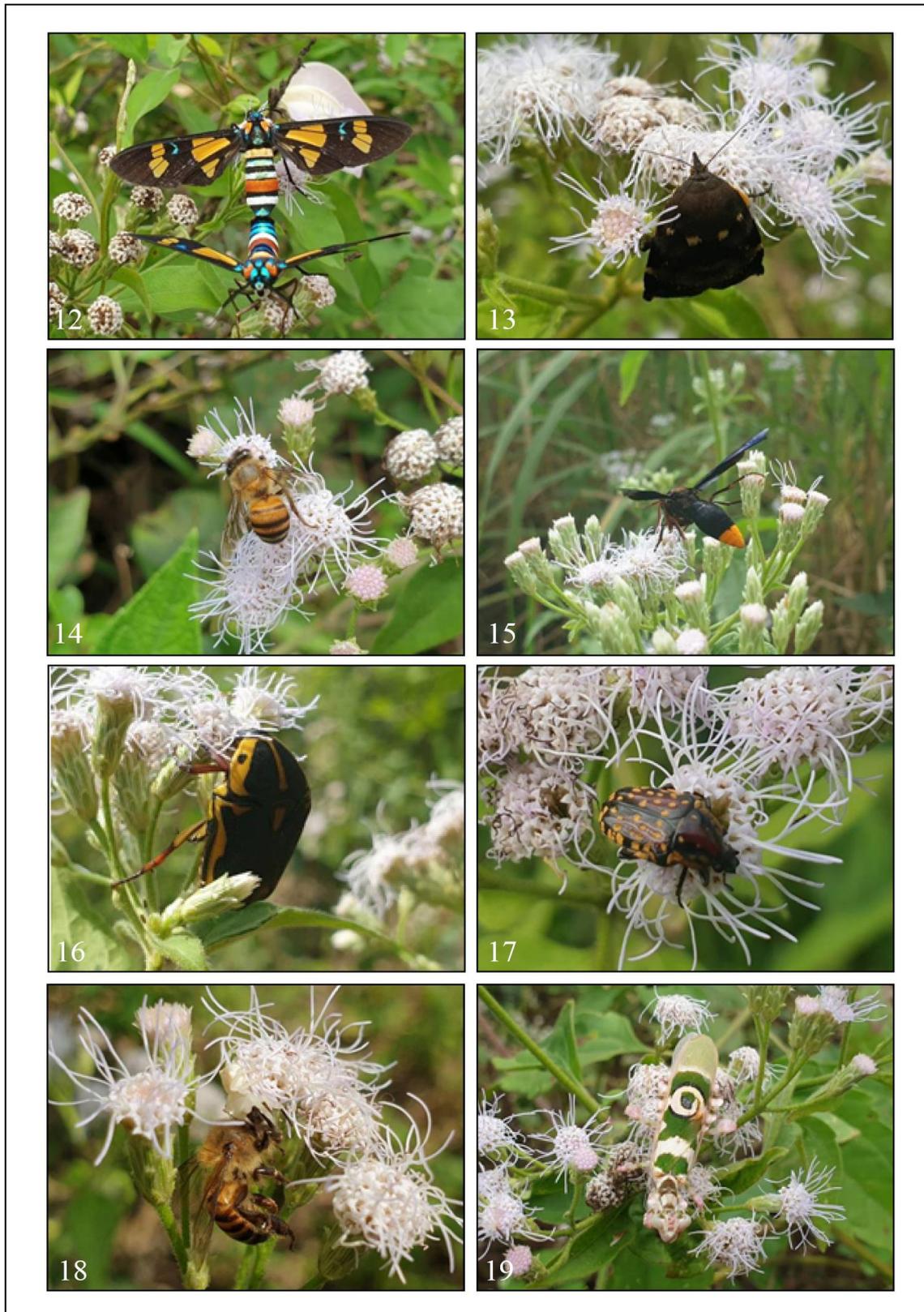


Figure 12 – Mating pair of *Euchromia folletii* (Guérin-Méneville, 1832) (= *formosa* (Boisduval, 1833)) is probably the most frequently observed moth species nectaring on *C. odorata* flowers; **Figure 13** – Members of the moth family Hyblaeidae are often diurnal and they often visit flowers, including those of *C. odorata*; **Figure 14** – Africanised Honey Bees (*Apis mellifica scutellata*) workers are the most frequent visitors and potential pollinators of *C. odorata* flowers; **Figure 15** – A wide range of wasps (Hymenoptera, Vespidae, Eumeninae) also visit *C. odorata* flowers; **Figure 16** – Chafers, like *Pachnoda cordata obsoleta* Schaum, 1844 (Coleoptera, Scarabaeidae, Cetoniinae) are equally attracted to fermented fruit and nectar; **Figure 17** – Others are mainly nectar-feeders, like the small chafer *Oxythyrea (Stichothyrea) guttifera* (Afzelius, 1817); **Figure 18** – Crab spiders (Araneae, Thomisidae) can easily hide among the lobed corollae until a prey, in this case a honey bee, is within reach; **Figure 19** – Flower Mantises (*Pseudocreobotra* spp.) (Mantodea, Mantidae) frequently hide between the flowers of *C. odorata*, waiting for a prey. It is fine example of adaptation, a change of habitat, induced by the availability of newly established food source.