Pollination syndrome of the African custard apple (Annona senegalensis Pers.) reveals reliance on specialized brood-site weevil pollinators in Annonaceae

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Abstract

The pollination syndrome of the African custard apple (*Annona senegalensis* Pers.; Annonaceae) was investigated to gain insights into the reproductive strategy of this multipurpose wild shrub. Flower visitors were collected and frequently surveyed in the morning on 30 flowers of 30 plants per site, at four sites across the Sudanian and Sudano-Sahelian climatic zones of Burkina Faso during the flowering season, from May to June. A total of nine species of insects including Coleoptera (Curculionidae, Scarabeidae), Hymenoptera (Formicidae) and Diptera (Tephritidae) were observed visiting flowers. Among the recorded insects, two sympatric species of weevil (Curculioninae, Ochyromerini, *Endaeus cf. floralis* and *Endaeus* sp.) were by far the most abundant (97% of specimens) and were observed on all the 120 flowers sampled. Both species were observed on the fleshy petals of the cantharophilous flowers of *Annona senegalensis* that they use as substrate for the development of larval stages. These observations echo with the ever-growing number of researches highlighting the major role of weevils in the pollination of the pantropical Annonaceae. Our study provides first evidence of brood-site mutualism between an Annonaceae species and its specialized weevils pollinators.

Introduction

The importance of insects is undeniable in the functioning of forest ecosystems where they play the roles of seed dispersal, pest regulation, herbivory, phytopathogen vectoring and a particular role of pollination in sustainability and continuity of ecosystem services. Plants and insects have developed a mutualistic interaction, plant providing nectar and/or pollen and insects ensuring pollination, and about 80 per cent of plants are pollinated by insects (Ollerton et al. 2011; Free 1993). Pollinating insects have developed innate perception abilities and attraction towards of flowers odor and color, and morphological and physiological adaptations to exploit the nectar hidden in the corolla (Willmer 2011). Adaptations have resulted in coevolution that leads to highly specialized mutualistic interactions between some pollinating insects and their host-plants. This relationship is manifested by a strong dependency of the plant upon its specialized pollinator for reproduction, on the one hand, and the insect upon its host-plant for food on the other hand.

Many studies reported that flowers of Annonaceae in the tropics were nearly exclusively visited and pollinated by beetles, and cantharophily (i.e. pollination by beetle) therefore was the overall prevailing pollination system in this family (Gottsberger 2012). The Annonaceae, with around 2,300-2,500 species distributed into 108 genera, is among the three largest basal Angiosperm families (Couvreur et al. 2011; Chatrou et al. 2012) and depends on insect pollination like most Angiosperms. *Annona senegalensis* Pers. (Annonaceae), is a widespread woody shrub in western Africa (PAO 2020). In West Africa, all parts namely the leaves, flowers, fruits, stem and roots of *Annona senegalensis* have several medicinal uses, by using of parched green fruits to relieve diarrhea and dysentery (Arbonnier 2009). The flowers, used for cooking sauce are rich in mucilage and (Millogo-Rasolodimby et *al*. 1996) and fruits with sweet pulp, eaten directly when ripe, are rich in glucose and Vitamin A, and constitute a real source of food for the local populations (Von Maydell 1983; Traoré et al. 2011; Zouré et al. 2021). It is a locally abundant and

scattered plant, common to the Sahelian to Guinean savannahs that grows on stony soils, on gravel banks and on fallow land and its distribution extends in tropical Africa, from Senegal to Sudan (Arbonier 2009). The flower structure of *Annona senegalensis* is recognized as sign of cantharophily among Annonaceae (i.e. pale color, fleshy petals, reversed flowers (Gottsberger 1999)), however, the pollination syndrome of this multipurpose species remains unknown to date. Recently in Burkina Faso, a total of 48 insects species belonging to 6 orders and 23 families were identified on flowers and fruits of *A. senegalensis* at different stages of development (Dao et al. 2022). Among these insects, Curculionidae species namely *Endaeus* spp. were found mainly on flowers and suspected to be pollinators. In its natural environment, *A. senegalensis* is observed with a rather abundant community of flower and fruit visiting insects, but their ecological function for the plant and their trophic interactions needs to be clarified (Dao et al. 2022), where *Endaeus* spp. commonly observed on the flowers seems to be the main pollinator of this plant. To find out the insect species which represent some mutualistic agents involved in pollination, the aim of this study is to describe the faunal community of *Annona senegalensis* flower insects in order to identify key pollinators.

Material And Methods

Study area

The study was conducted in four sites equitably distributed across the Sudanian and Sudano-Sahelian climatic zones of Burkina Faso (Fig. 1), where the plant is spontaneous and abundant. In the Sudanian zone, survey was carried out at two sites: the Dindèrèsso classified forest (N 11°12’38”, W 004°24’43”) and Dafra fallow (N 11°07’18”, W 004°14’50”), located to the North-west and the South of Bobo-Dioulasso city. The sites of Toroba classified forest (N 12°29’14”, W 003°15’35”) and Koussiri fallow (N 12°33’09”, W 003°15’47”), located about 40 km and 30 km, respectively, to the East of Dédougou city, were chosen in the Sudano-Sahelian zone. Fallows were near cultivated fields, where farmers often use pesticides. In contrary, classified forest sites were distant from cultivated areas. The climate is tropical with two contrasting seasons in both study zones: a dry season (from October to April) and a rainy season (from May to September). The two zones differ in terms of environmental conditions (Fontès et Guinko 1995) (Table 1).

Table 1
Biophysical characteristics of climatic zones in the study area

Parameters	Sudano-sahelian	Sudanian
Annual rainfall (mm)	500–900	800–1100
Number of rainy months	May/June- October	May- October
Temperature range (°C)	22–32	25–30
Mains rivers of the hydrographic system	Mouhoun	Comoé and Mouhoun
Main vegetation types	Woodlands and savannahs	Gallery forests and savannahs
Main soil types	Taw mineral soils and undeveloped soils; vertisols and eutrophic brown soils; tropical ferruginous soils; hydromorphic soils.	Tropical ferruginous soils; hydromorphic low ferruginous soils; soils rich in iron and manganese oxides and hydroxides; soils of the top of the plateau ridges; sandy soils.

Source: Adapted from Millogo-Rasolodimby et *al.* (1996).

Sampling Of Insects

The sampling was carried out from May to June 2020, corresponding to the flowering phenology of *Annona senegalensis* according to Arbonier (2009). Insect captures were done on the Dindèrèsso classified forest and the Dafra reserve from May to August 2020. As for Toroba national forest and Koussiri reserve, they were sampled from June to October 2020. At each date of sampling, 30 flowering plants of *Annona senegalensis*, at least 100 m apart from each other and growing in uncultivated areas were selected randomly. The insects were collected according to the method described by Grouzis et Sicot (1980). Thus, on each plant at the stage of flowering, 30 flowers per trees on 30 trees per site were chosen randomly. The capture of insects was done by immersing the flowers carrying insects in 70% ethanol. Insects collected were immediately stored in bottles containing 70% ethanol. Collection of insects on flowers concerned the diurnal insects and took place between 7 a.m. and 10 a.m. corresponding to the periods of intense activity of the insects according to Kouyaté et *al*. (2016); Tchuenguem et al. (2014) and Tchindébé et al. (2018).

Observation Of Insect Behavior

In the Sudanian zone where the insects are more abundant on flowers, we monitored the behavior of insects on 30 flowers of 30 plants by site, from the beginning to the end of flowering period (e.g. May to August, in the sites of Dafra and Dindèrèsso). The adapted method from Boussim et al. (1993) consisted in direct observation of insects visiting flowers. The species of insects that come on the flowers was recorded, the number of individuals, the position occupied on the flower (inside or outside) by each individual, whether the individuals visit the floral chamber or not, the number of minutes spent on the flower, the presence of damage on the flower, the presence of pollen carried by insects and the visit of flowers of different plants were recorded. The observation of each flower lasted 5 minutes. Observation of insects on flowers took place between 7 a.m. and 10 a.m. every 10 days on each site from May to June in addition to some observations made in the morning, at noon and in the evening to survey potential other flower visitors with specific timed phenology.

Identification Of Insects

Insects collected on *A. senegalensis* flowers were counted and examined in the laboratory under a binocular microscope using previously identified specimens by a taxonomic entomologist. Identification of these insects was performed by using the taxonomic keys of Villiers (1943, 1977); Pihan (1986); Cherix (1986); Stanek (1984) and Bland (1947). The weevils were identified by comparisons with reference collections housed at the Natural History Museum (London, United Kingdom) and the Museum National d'Histoire Naturelle (Paris, France).

Data analysis

Statistical analyses were performed using R software version 4.0.3. Fisher's Exact test were used to determine if there is a difference in the insect abundance and Chi-squared test was used for richness of insects in climatic zones, at the threshold of P = 0.05.

Results

Identification and Diversity of insect species on flowers

Nine insect species belonging to 3 orders (Coleoptera, Hymenoptera and Diptera) and 4 families (Curculionidae, Formicidae, Scarabaeidae and Tephritidae) were identified on the flowers of *A. senegalensis* across the two climatic zones (Table 2). The weevils recorded consisted in two closely related species of *Endaeus* (Curculioninae, Ochyromerini). A first species, the larger one, is closely related to *E. floralis* Marshall, 1907 (here after called *E. cf. floralis*). The second species, the smaller one, was not identified yet to species level in our current knowledge and is provisionally called *Endaeus* sp. 1. The two species co-occur among the sampling sites (Fig. 2). Preliminary assessment of relative abundance of samples indicates that *Endaeus cf. floralis* is 1/3 more abundant than *Endaeus* sp. 1. As far as the two

species are very close morphologically and because of difficulty to distinguish them taxonomically, they were referred together as *Endaeus* spp. in the following text (Table 2).

Table 2
Diversity of insect species found on flowers according to their abundance and their distribution by site

			Number of individuals/sites			
Order	Family	Species	Sudanian zone		Sudano-Sahelian zone	
			Dafra	**Dinderesso**	**Koussiri**	**Toroba**
Coleoptera	**Curculionidae**	*Endaeus cf. floralis* & *E.* sp1	385	1189	189	189
	Scarabaeidae	*Myodermum alutaceum* (Afzelius, 1817)	1	2	1	8
Diptera	**Tephritidae**	*Ceratitis cosyra* (Walker, 1849)	-	-	1	-
Hymenoptera	**Formicidae**	*Brachyponera senaarensis* (Mayr, 1862)	1	-	-	-
		Camponotus maculatus (Fabricius, 1782)	-	1	-	-
		Crematogaster sp	3	-	-	-
		Messor galla (Mayr, 1904)	1	-	-	4
		Trichomyrmex abyssinicus (Forel, 1894)	18	1	6	13
		Total number of individuals	409	1193	197	214
		Number of species	07	05	05	05

Frequency, Abundance And Distribution Of Insects On Flowers Across Climatic Zones

Insects captured on the flowers of *A. senegalensis* are not so diversified. Among the nine species found on the flowers of *Annona senegalensis*, *Endaeus* spp. (Curculionidae) were by far the most common species, and met on all the flowers in all the four sites. Upon the total of 2,013 insects collected on flowers, 1,952 individuals were *Endaeus* spp., representing 97% of all the insects sampled. *Endaeus* spp.

are also the most abundant species on flowers with an average of 26 ± 21 (standard deviation) individuals per flower in the Sudanian zone and 6 ± 5 in the Sudano-sahelian one. The greatest number of insects on a flower was observed in the Sudanian zone, in the Dindèrèsso site, with a total number of 94 individuals of *Endaeus* spp. on a single flower. It is sometimes accompanied by Formicidae (in particular *Trichomyrmex abyssinicus* and *Messor galla*). Their number fluctuates between 1 and 2 individuals per flower and can exceptionally reach 4 individuals. The Scarabaeidae, *Myodermum alutaceum* was also observed in all sites but at a very low frequency, rarely exceeding 1 individual per flower whatever the site.

Although there was a large difference between the abundance of insects on flowers in the two climatic zones (Fisher's Exact test: *p-value* 1.15 e-09), we found no significant difference of the species richness between these zones (Chi-squared test: X-squared = 0.33333, df = 1, *p-value* > 0.56). Dindèrèsso, in the Sudanian zone, is the site with the highest mean number of insects collected on flowers. These insects and especially *Endaeus* spp., were more abundant in the Sudanian zone than the Sudano-Sahelian zone, where the lowest quantities of insects are recorded on flowers in the sites.

Behavior Of Insects On Flowers

Observation of insect behavior shown that *Endaeus* spp. went from flower to flower, especially at the end of the anthesis phase. At this stage, the whole group of *Endaeus* of a flower disperses and they can be observed flying to other flowers of the same plant or other plants. These insects have also been observed on flowers with pollen on the legs or body.

The presence of *Endaeus* spp. on flower was always associated with feeding damages on the internal faces of the petals (Fig. 3a&b). These beetles were observed hidden, mating and feeding in the floral chamber, their rostrum embedded in the petals (Fig. 3c). Eggs are deposited in holes also dug in the internal parts of the petals (Fig. 3d). Larval development takes place in the fleshy tissues of the petals. They make holes when they emerge as adults from the petals, suggesting that metamorphosis takes place in the soil.

The scarab beetle, *Myodermum alutaceum* was also observed at all sites. This large beetle removes the floral pieces and enters the flower (Fig. 3e). No serious damages were recorded from this species. It was only observed opening the flowers, trying to access reproductive organs. The larval biology of this species has not been checked, but its development does not take place in the flowers. As far as ant species are concerned, they were always observed in low number, and mostly outside the flower pollination chamber (Fig. 3f).

The period of *A. senegalensis* flowering and the visit of insects on flowers correspond to the months of May-June, the beginning of the rainy season in the study area. Insects only visit the plant when flowers are blooming. Flower buds were not hosting any insects. Most insects visiting flowers were found during a large part of the blooming, their visits only starting or ending slightly after and before this period. Only

Endaeus spp. were observed to visit flowers throughout the entire flowering period of *A. senegalensis* (Fig. 4).

Discussion

Previous studies showed the presence of many insects in connection with the phenological stages of *A. senegalensis* in Burkina Faso (Dao et al. 2022). The diversity of insects that visit flowers of *Annona senegalensis* is relatively low. In their investigations, Lau et al. (2016) recorded thirteen different floral visitors belonging to five orders in one Annonaceae species, namely *Goniothalamus tapisoides* in Borneo during two consecutive years of observation. In Neotropical Annonaceae, species from several beetle families such as Nitidulidae, Curculionidae, Staphylinidae, and Chrysomelidae are involved in pollination of the cantharophilous flowers, often forming diversified species assemblages on a single host plant (Gottsberger 1999; 2012). With only Curculioninae and in a lesser extent Scarabaeidae, *A. senegalensis* has a much more restricted range of flower visitors than that is known in other species of this family from other regions. This species has two main floral visitors: *Endaeus cf. floralis* and *Endaeus* sp. 1, which echoes with the growing body of studies highlighting the role of specialized weevils, in particular species of among the tribe Ochyromerini, in the pollination of this family (Gottsberger 1999; Saunders 2020). The absence of differences in communities between sites was observed further strengthen, the hypothesis that *A. senegalensis* relies on highly specialized flower visitors involving these weevils to ensure its pollination. In weevils, there is a strong phylogenetic niche conservatism at genus level for lineages engaged in brood site pollination mutualism with plants (Toon et *al*. 2020; Franz & Valente 2005; Haran et al. 2021). So, if a pollination mutualism is highlighted for a weevil species, it is likely that congeneric species are implicated in similar relationships with plants. As such, it is likely that the *Endaeus* spp. which often carrying pollen and can visit several flowers of different plants, act as specialized pollinators of this plant since this relationship was demonstrated for several congeneric species in Asia (Saunders 2020).

The structure and physiology of flowers in *A. senegalensis* also agree with the features associated with specialized cantharophily in Annonaceae. The production of scents, although not identified in details in the context of this study, has been widely documented in this family as mean of attraction of beetles (Deroin 1989; Gottsberger & Silberbauer-Gottsberger 2014; Gibernau 2020). In *Xylopia championii* Hook.f. & Thomson, for example, the peak of production of a fruity scent during the pistillate phase coincidates with the presence of a specific *Endaeus* on flowers suggesting that these odours attract only a few species involved in pollination (Ratnayake et al. 2007). The fleshy petals of *A. senegalensis* are probably the most suggestive of an adaptation of the plant to improve success of a cantharophilous pollination (Gottsberger & Silberbauer-Gottsberger 2014). First, these thick petals play a role of protection for the reproductive tissues by excluding the larger and non pollinating species to enter (Gottsberger 1999; Gottsberger & Silberbauer-Gottsberger 2014). These more or less curved petals also form a pollination chamber where pollinators may stand protected (Gottsberger 1999; Gottsberger & Silberbauer-Gottsberger 2014; Saunders 2020). In *A. senegalensis*, the morphology of the pollination chamber is remarkably aligned with those of its *Endaeus* pollinators since up to around one hundred of them could be lodged in a single flower of a few centimeters. Fleshy petals are also a source of food for pollinators in

Annonaceae, as they contain food bodies corresponding nutrient rich tissues (Gottsberger 2012). In *A. senegalensis*, petals are intensively perforated by adults of *Endaeus* spp., that leave the typical feeding damages encountered in weevils. No other insect visiting the flowers of this anon was observed consuming the tissues of petals, suggesting that this food resource is aligned with requirements of the weevils.

A salient result of this study is the observation of the breeding site for a weevil pollinating an Annonaceae. This was only suggested based on observation of oviposition behavior on petals (Saunders 2020). By reporting oviposition and larval development of *Endaeus* spp. in the fleshy petals of the plant where they pollinate, we confirm that Annonaceae contains examples of brood-site pollination mutualism. As such, the anon-weevil pollination mutualism can be classified among the mutualism reported between several monocot families (Araceae, Arecaceae, Cyclanthaceae) and derelomine weevils (Franz & Valente 2005), between cycads (Cycadaceae, Stangeriaceae and Zamiaceae) and several weevil lineages (Belidae, Brentidae, Molytinae), (Toon et *al*. 2020), and more generally the classical examples of fig-figwaps and Yucca-Yucca moth systems (Pellmyr 2003; Herre et al. 2008). Future studies should explore the degree of specialisation of *Endaeus* spp. on their host-plant and whether *A. senegalensis* relies only in a very specialized pollination system involving weevils alone or if it can cope with anemophily and general entomophily as well. Ants may be involved in the pollination of this species, but they are quite rare in the flowers and rarely visit the pollination chamber. Their role in pollination of *Annonaceae* is ambiguous and varies between species studied (Ratnayake et al. 2006; Mertens et al. 2018). They may however, like *Myodermum alutaceum* (Scarabaeidae), be part of the assemblage of generalist pollinators generally associated with weevil-based pollination systems (Gottsberger 2012; Lau et al. 2016; De Medeiros et al. 2019) and provide a minor contribution to pollination.

The abundance of *Endaeus* spp. is lower in the Sudano-Sahelian zone than in the Sudanian zone. This could be related to climatic conditions such as temperature, rainfall, relative humidity, the soil type and vegetation which differ in the two climatic zones. Indeed, in the Sudano-Sahelian climatic zone, the temperature is slightly higher, the rainfall is lower and the rainy season is slightly shorter than in the Sudanian zone. In addition, there are soils such as soils rich in iron and manganese oxides and hydroxides, soils of the top of the plateau ridges, sandy soils and gallery forests present in the Sudanian zone but absent in the Sudano-Sahelian zone where we also find taw mineral and undeveloped soils, vertisols, eutrophic brown soils and woodlands. However, insects on flowers could be more abundant in the classified forest sites due to the abundance of vegetation, and therefore the abundance of food providing some better living conditions for the insects affecting the number of insect species. Sauvion et *al*. (2013) showed that insect species may be limited or favored by environmental factors, which could impact their presence or absence in a given area.

Conclusion

The flowers of *Annona senegalensis* are visited by a narrow range of insects among which two species of weevils were identified as dominant specialized pollinators. Physiological adaptations of this plant and

the observation of breeding sites for immature stage of these weevils echoes in all respect to the pollination mutualism interactions reported in Annonaceae and those involving brood-site in other plant lineages. The description of this specialized pollination mechanism opens new avenues for the exploration of pollination ecology in African Annonaceae and its consequences for reproductive success and fruit set in this diversified tropical family.

Declarations

Competing interests

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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Figures

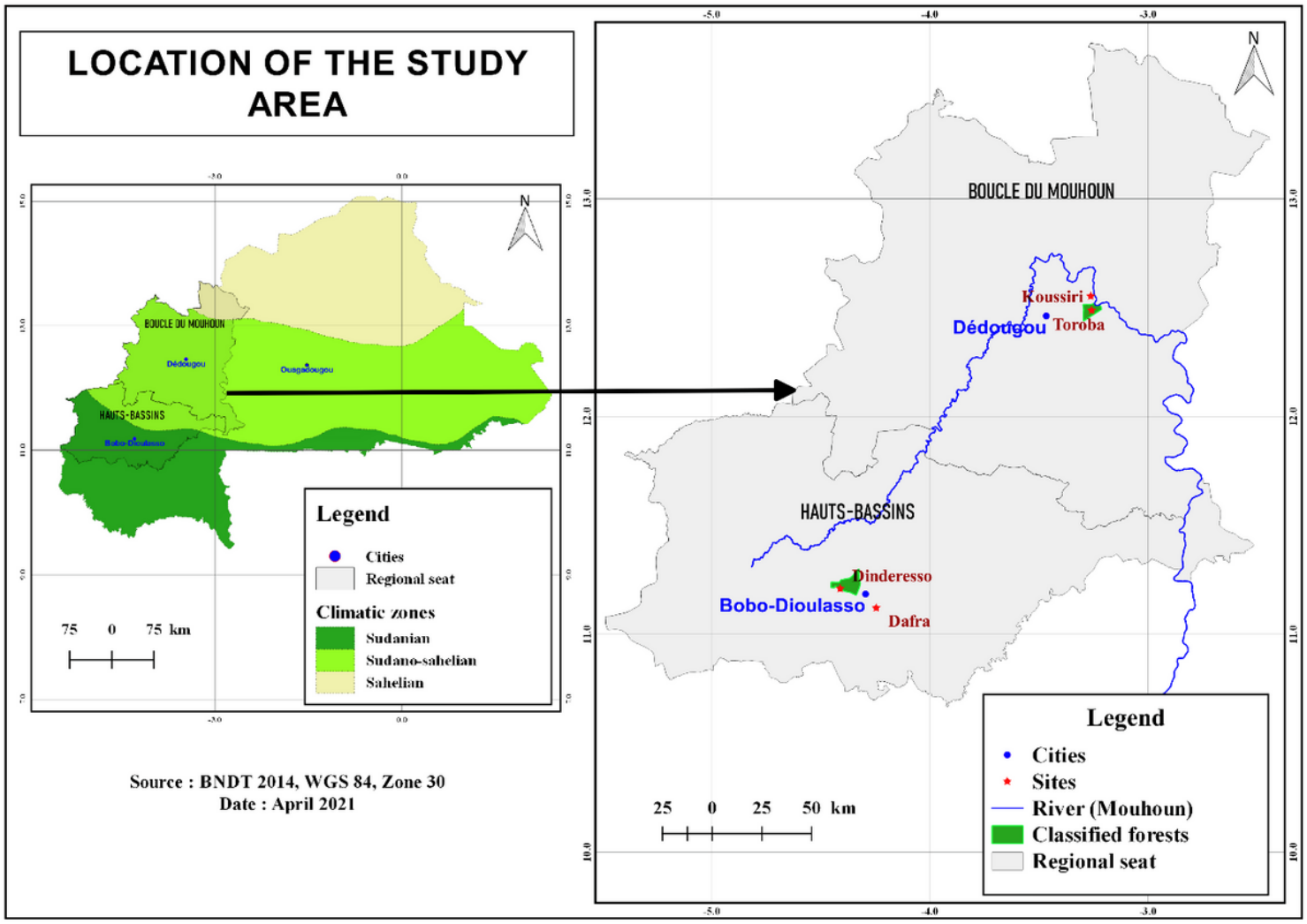

Figure 1

Map of the study areas in Sudanian and Sudano-Sahelian zone in Burkina Faso

Figure 2

Habitus dorsal of male specimens of *Endaeus cf. floralis* (left) and *E.* sp. 1 (right) main floral visitors of *A. senegalensis* in Burkina Faso. Scales bar: 1 mm.

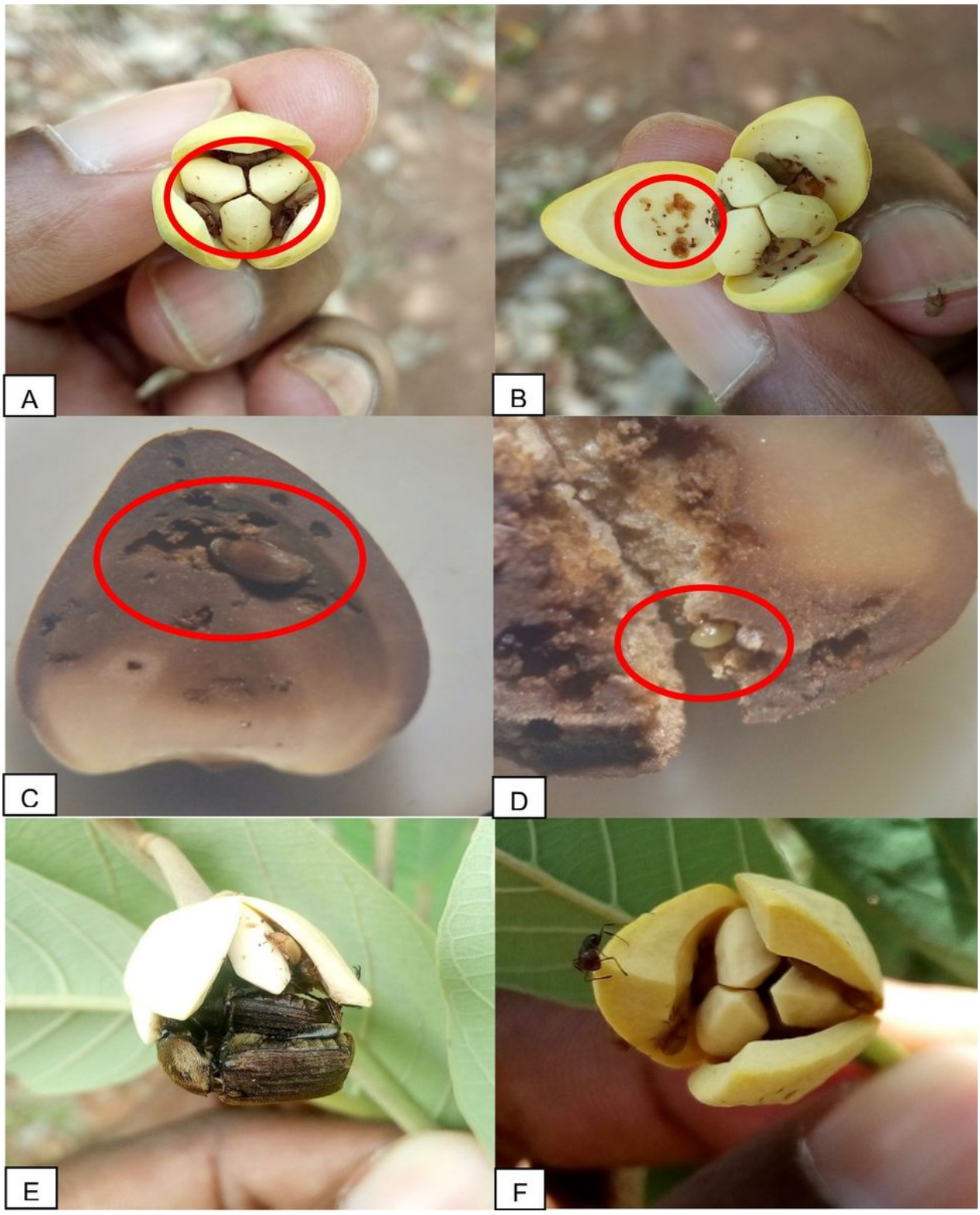

Figure 3

Insects visiting flowers of *Annona senegalensis*; A: *Endaeus* spp. lodged in the pollination chamber; B: Hole in the petals made by *Endaeus* spp.; C: The head of *Endaeus* spp. embedded in the petals stored in ethanol; D: Egg of *Endaeus* spp. laid in the internal part of the fleshy tissue of petal stored in ethanol; E: *Myodermum alutaceum* male and female (large insects) mating in a flower near *Endaeus* spp, visiting the same flower; F: *Crematogaster* sp. observed outside the flower with *Endaeus* spp. inside the flower.

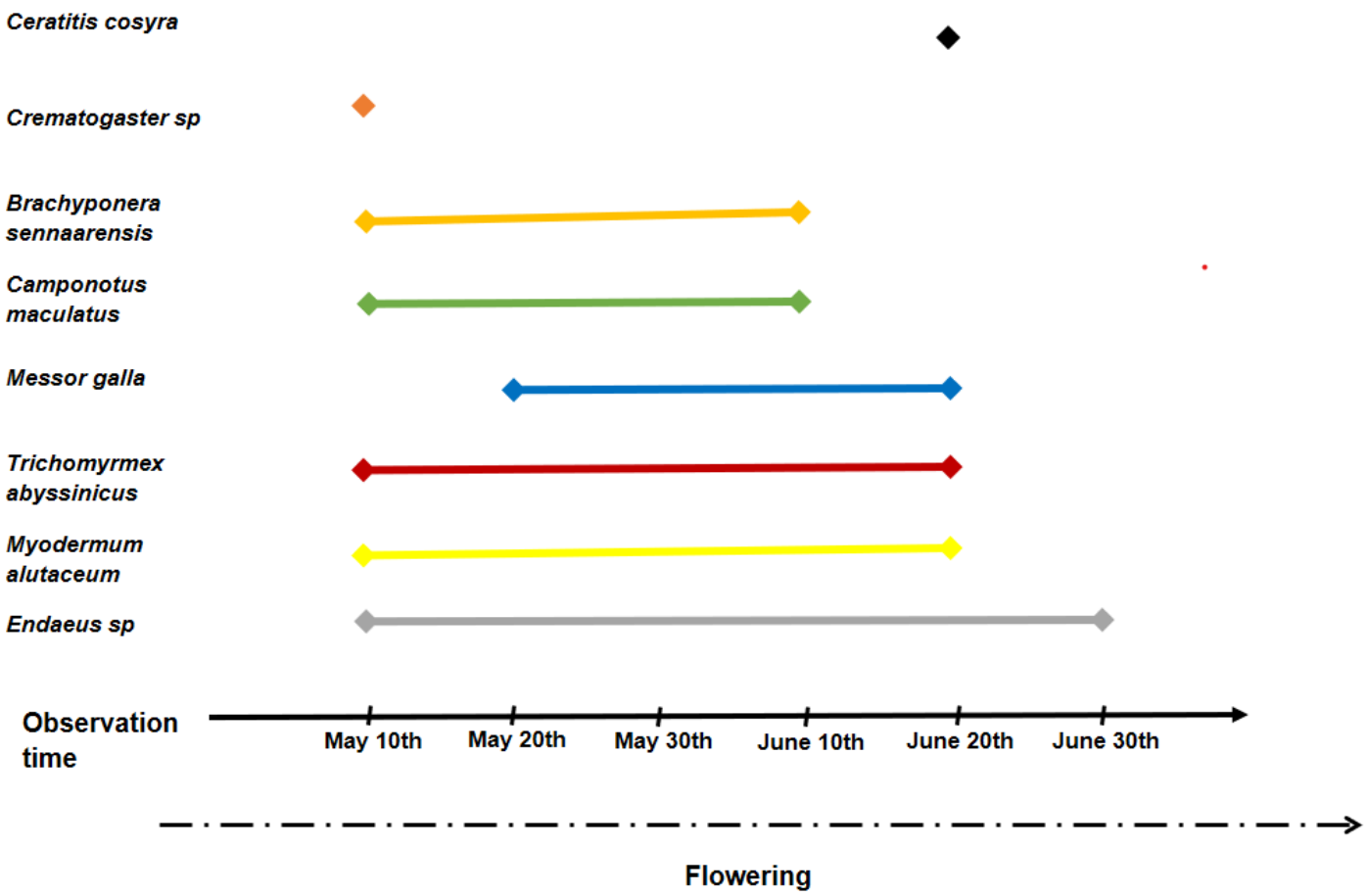

Figure 4

Visit Periods of insect species on the flowers from May to June