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Natalia Medina-Serrano, Martine Hossaert-Mckey, Aly Diallo, Doyle McKey. Insect–flower interactions, ecosystem functions, and restoration ecology in the northern Sahel: current knowledge and perspectives. *Biological Reviews*, In press, 10.1111/brv.13170 . hal-04872062

HAL Id: hal-04872062

<https://hal.science/hal-04872062v1>

Submitted on 7 Jan 2025

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Insect–flower interactions, ecosystem functions, and restoration ecology in the northern Sahel: current knowledge and perspectives

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ABSTRACT

Actions for ecological restoration under the Great Green Wall (GGW) initiative in the northern Sahel have been plant focused, paying scant attention to plant–animal interactions that are essential to ecosystem functioning. Calls to accelerate implementation of the GGW make it timely to develop a more solid conceptual foundation for restoration actions. As a step towards this goal, we review what is known in this region about an important class of plant–animal interactions, those between plants and flower-visiting insects. Essential for pollination, floral resources also support insects that play important roles in many other ecosystem processes. Extensive pastoralism is the principal subsistence mode in the region, and while recent analyses downplay the impact of livestock on vegetation dynamics compared to climatic factors, they focus primarily on rangeland productivity, neglecting biodiversity, which is critical for long-term sustainability. We summarise current knowledge on insect–flower interactions, identify information gaps, and suggest research priorities. Most insect-pollinated plants in the region have open-access flowers exploitable by diverse insects, an advantageous strategy in environments with low productivity and seasonal and highly variable rainfall. Other plant species have diverse traits that constrain the range of visitors, and several distinct flower types are represented, some of which have been postulated to match classical “pollination syndromes”. As in most ecosystems, bees are among the most important pollinators. The bee fauna is dominated by ground-nesting solitary bees, almost all of which are polylectic. Many non-bee flower visitors also perform various ecosystem services such as decomposition and pest control. Many floral visitors occupy high trophic levels, and are indicators of continued functioning of the food webs on which they depend. The resilience of insect–flower networks in this region largely depends on trees, which flower year-round and are less affected by drought than forbs. However, the limited number of abundant tree species presents a potential fragility. Flowering failure of a crucial “hub” species during exceptionally dry years could jeopardise populations of some flower-visiting insects. Furthermore, across Sahelian drylands, browsers are increasingly predominant over grazers. Although better suited to changing climates, browsers exert more pressure on trees, potentially weakening insect–flower interaction networks. Understanding the separate and combined effects of climate change and land-use change on biotic interactions will be key to building a solid foundation to facilitate effective restoration of Sahelian ecosystems.

Key words: biotic interactions, drylands, Ferlo region, flower-visiting insects, plant–animal interactions, restoration, Sahelian ecosystems, semi-arid savannas.

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I. INTRODUCTION

The Sahel is among the world's most environmentally degraded regions and is highly vulnerable to climate change. Faced with the prospect of accelerated degradation by climate change, demographic growth, and land-use change, initiatives have been launched with the objective of restoring the region's ecosystems and the services they provide to people. Under the auspices of the United Nations Convention to Combat Desertification (UNCDD) (since 1996) and the pan-African initiative the Great Green Wall (GGW) (since 2007), numerous projects have attempted to contribute to this objective. Too often, however, actions have been grounded in sectoral approaches: water, vegetation, and livestock are treated as separate problems and managed by different agencies. There is a need for integrative approaches that link all components of ecosystem functioning.

Among the components that have been neglected are plant–animal interactions. Although crucial to ecosystem functioning, these interactions have only recently begun to receive attention in efforts to restore degraded ecosystems. As Genes & Dirzo (2022) concluded, approaches to restoration have typically been centred either on plants or on animals, with little consideration of their interactions.

In the Sahel, efforts to restore ecosystems have been strongly plant centred, particularly on trees, with little attention given to grasses and forbs. Furthermore, these efforts have concentrated on actions such as the planting of massive numbers of tree seedlings (mostly of local species that provide products useful to humans), with less attention given to natural regeneration and to the interactions on which it depends.

Many plant–animal interactions are affected by the changes in climate and in land use that drive ecosystem degradation in the Sahel. Responses of plants to mammalian herbivores affect vegetation dynamics. Interactions between plants, mammalian herbivores, and coprophagous insects drive decomposition and nutrient cycling; all these interactions change when livestock replace native herbivores, as they have in the Sahel today (Hempson, Archibald & Bond, 2017), and when livestock are treated with parasiticides that persist in their excrement (Ambrožová *et al.*, 2021). Both wild and domestic vertebrates disperse seeds, sometimes contributing to natural regeneration but often favouring the spread of invasive plants (Kebede & Coppock, 2015). The diverse fauna of ground-dwelling granivorous birds and rodents in the Sahel depends on the soil seed bank, which can be depleted by grazing pressure that is too intensive or that occurs at the wrong time (Zwarts, Bijlsma & van der Kamp, 2023b).

We focus here on interactions between flowers and flower-visiting insects. Several considerations justify this choice. First, flower-visiting insects are a strategic point of entry for studying insect biodiversity as a whole. Insect–flower interactions involve and affect a broad swath of the taxonomic and functional biodiversity of insects, the most diverse group of terrestrial organisms. As flower-visiting insects are involved in many other biotic interactions (Vizentin-Bugoni *et al.*, 2018), the status of their communities can serve as an indicator of ecosystem health (Kevan, 1999). Flower-visiting insects provide not only the pollination services on which many plants depend; they also contribute to many other ecosystem functions. Floral nectar provides fuel for insects that are parasitoids and predators of other arthropods, regulating their populations. Because they occupy high trophic levels, parasitoids and predators should be particularly good indicators of ecosystem health, as they provide evidence for the continued presence of the community of arthropods on which they depend (Brock, Cini & Sumner, 2021). Secondly, in addition to their diverse roles in ecosystem functioning, flower-visiting insects contribute directly to human livelihoods, pollinating fruit trees and crop plants (Bergeret & Ribot, 1990). Third, there are huge gaps in our knowledge of plant–pollinator interactions throughout Africa (Rodger, Balkwill & Gemmill, 2004; Archer *et al.*, 2014). Studies of pollination networks in the tropics are strongly biased with respect to region (most studies are in the Neotropics) and habitat (most studies are in forest) (Vizentin-Bugoni *et al.*, 2018). Fourth, although arthropods comprise over 90% of terrestrial species (Briggs, 2016), insects and other arthropods are often overlooked in biodiversity studies. For example, a review of animal biodiversity in the Sahara–Sahel and threats to its conservation (Brito *et al.*, 2016) includes a brief mention of only one insect group, dragonflies. We found a synthesis of adaptations and biodiversity patterns in the Sahel of one economically and ecologically important group, dung beetles (Coleoptera: Scarabaeidae). Sahelian dung beetles have evolved short life cycles and flexible nesting behaviour, advantageous in these extreme environments (Rougon & Rougon, 1991). If similar information exists for other insect groups in the Sahel, it has not yet been synthesised. Finally, the two main drivers of degradation in the Sahel, climate change and land-use change, are known to affect insect–flower interactions elsewhere (Filazzola *et al.*, 2020; Bascompte & Scheffer, 2023).

Within the Sahel, there is a strong north–south gradient in annual rainfall, ranging from about 100–200 mm in the north, where the Sahel gives way to desert, to about 500–600 mm at its southern limit, where it grades into Sudanian savannas. We focus herein on the northern Sahel. We use this term to refer to the part of the region where annual precipitation is too low (< about 350 mm) and unreliable to permit crop agriculture, so silvopastoral subsistence systems, dominated by extensive pastoralism, replace the agrosilvopastoral subsistence systems that characterise the more humid southern Sahel. For rainfall isohyets and climate zones for West Africa, see Maps 3 and 4 in OSS (2019).

The northern Sahel also corresponds to the zone initially targeted by the GGW initiative, the framework for many ecological restoration efforts in the region. We focus particularly on literature for the Ferlo region of northern Senegal, which has been the subject of more research and more restoration initiatives than other parts of the northern Sahel, and where our own fieldwork was conducted.

(1) Objectives of this review

We aim to summarise what is known about insect–flower interactions in the northern Sahel and how they may be impacted by changes in climate and land use. We first outline the composition and diversity of the plants that provide resources for flower-visiting insects, describe the nature of these resources (nectar, pollen, oil) and give information on floral traits that either limit the range of insects with access to floral resources of different plants, owing to morphological (or other) mismatches, or that allow access to a wide range of visitors. We also describe flowering phenology, which in many species is shaped by the harsh abiotic conditions of these environments. In parallel, we outline the community composition and diversity of the insects that visit flowers in these ecosystems, and describe the traits that enable some insects to exploit concealed (or otherwise limited-access) floral resources and restrict others to exploiting exposed resources. We assess the roles of different insect groups in pollination and other ecosystem services, and describe what is known about the phenology of flower-visiting insects.

In this study, we offer tentative generalisations about the structure and functioning of insect–flower networks in arid and semi-arid northern Sahelian savannas, identifying sources of resilience and of vulnerability to threats posed by human land use and by climate change. Our main goal is to identify gaps in our knowledge of insect–flower interactions in the region and outline research priorities. We hope to lay the groundwork for studies that identify and monitor indicators of the status of insect–flower interactions in the northern Sahel. Knowing how these indicators respond to changes in climate and in land use will be essential for designing actions to conserve, and if necessary, restore, the integrity of these interactions and the ecosystem functions and services they provide.

(2) Methods

We conducted a scoping review, a method appropriate to the scattered and fragmentary nature of the literature on this topic and to our goal of identifying knowledge gaps (Munn *et al.*, 2018). The taxonomic and thematic scope of our review was very broad, covering diverse plant and insect groups, and facets of their interactions ranging from resources and phenology to their interconnections with other interactions in ecosystems. Criteria for inclusion of literature were thus too expansive for an exhaustive systematic review to be feasible. Furthermore, a narrowly focused systematic review was inappropriate, given the paucity of studies that centre on

insect–flower interactions in the region. Scoping reviews are useful for examining emerging evidence, for identifying and analysing gaps in the knowledge base (Munn *et al.*, 2018), and for generating hypotheses (Tricco *et al.*, 2016).

Many plant species of the northern Sahel are wide-ranging, and we included studies of their interactions with flower-visiting insects elsewhere in their geographic range when these were available. We also drew on emerging results of our own studies.

In our literature search, conducted using *Google Scholar*, we first established a list of common herbaceous and woody plant species in the northern Sahel. These lists were compiled from Guissé *et al.* (2023) and Miede *et al.* (2010) for the flora of the Ferlo of northern Senegal. Composition of vegetation in this region is similar to that of other sites in the northern Sahel (e.g. Bille & Poupon, 1972; Breman & de Ridder, 1991). We extracted information on the geographic distribution of each species from *Plants of the World Online* (POWO, 2024). We consulted Borokini *et al.* (2023) to establish whether each species is native to, naturalised, or invasive in the Sahel. We then identified authoritative recent reviews on the floral biology of the families represented and on the biology of flower-visiting insect orders and families found in the region, including their life cycles and the resources they depend on in addition to flowers. We also identified authoritative cross-taxon comparative reviews of specific topics in floral biology [e.g. ambophily (Abrahamczyk, Struck & Weigend, 2023), presence/absence of floral nectaries (Bernardello, 2007), occurrence of monoecy and dioecy (Renner, 2014), and floral symmetry (Reyes, Sauquet & Nadot, 2016)], and consulted recent reviews of pollination syndromes and pollinator networks (Ollerton *et al.*, 2009, 2015; Rosas-Guerrero *et al.*, 2014; Aguilar *et al.*, 2015). We then surveyed these reviews for references to species occurring in the Sahel or close relatives of these species. We also conducted separate searches for each plant species, using terms such as “pollination”, “flower”, and “floral biology”. We summarise the principal results of our research in the main text, tables, and figures. Details for particular plant species are presented as online Supporting Information in Tables S1 and S2. Although we do not claim that this information exhaustively covers the literature, it is evident that there are many gaps in knowledge. Knowledge gaps are even greater for insects, with almost no information available at the species level, that is the level that is pertinent for analysis of biotic interactions.

Insects are not the sole pollinating animals in the region; a few vertebrate species may be important pollinators of some plants. Diop, Diop & Ndiaye (2024) recorded one species of sunbird (Nectariniidae) in the Ferlo, the pygmy sunbird (*Hedydipna platyura*), as well as single species of each of two families (Coliidae, Pycnonotidae) that occasionally feed on nectar but are primarily frugivorous (Symes & Downs, 2001). Like insects, vertebrate flower visitors are vulnerable to climate change and land-use change in the Sahel. Cresswell *et al.* (2007) found *H. platyura* to be among the many bird species whose populations dramatically declined over an eight-year period in a rapidly degrading Sahelian woodland in northern

Nigeria. Fruit bats (Pteropodidae) may also be pollinators in the region. One tree common in the Ferlo, the baobab (*Adansonia digitata*, Malvaceae), is known to be pollinated by fruit bats elsewhere in its range (Djossa *et al.*, 2015). However, fruit bats decrease in diversity and abundance with increasing aridity from Sudanian to Sahelian savannas (Lassen *et al.*, 2017) and are very rare in the northern Sahel (Cosson, Tranier & Colas, 1996). As in the driest parts of its range in southern Africa (Taylor *et al.*, 2020; Karimi *et al.*, 2022), baobab in the northern Sahel may be pollinated not by bats but by hawkmoths. The status of fruit bats in the northern Sahel and their role in the pollination of baobab are questions deserving investigation. Another “bat-pollinated” tree, *Parkia biglobosa* (Fabaceae: Mimosoideae) – found in the more humid Sudanian and Guinean savannas south of the Sahel – is pollinated primarily by honeybees in the drier parts of its range in Burkina Faso (Lassen *et al.*, 2017). Increased drought with climate change is likely to lead to southward shifts in the range both of trees such as *P. biglobosa* and *A. digitata* that fruit bats depend on (Maranz, 2009; Lassen *et al.*, 2017) and of the bats themselves. In view of the limited importance of birds and bats as pollinators in the northern Sahel, we treat only insect flower visitors in this review.

II. STATE OF KNOWLEDGE ABOUT FLORAL RESOURCES AND THEIR PHENOLOGY IN THE NORTHERN SAHEL

(1) Floristic composition in the northern Sahel and characterisation of floral resources

The flora of the Sahel is rather poor, with approximately 1500 species of flowering plants in an area of 3 million km². The region is transitional between the Sahara and the wetter Sudanian savannas further south, and only a few species (about 40) are endemic to the Sahel. Drier sites within the region are occupied by Saharan elements of the flora, while species with Sudanian affinities are restricted to wetter sites (Le Houérou, 1989). Most species are wide-ranging, and some are pantropical. A substantial proportion of the common forbs were introduced into Africa from the Neotropical and Indomalayan regions, often in the pre-colonial and colonial periods (Borokini *et al.*, 2023). Many of these are naturalised, and some are invasive.

Table 1 describes the floral traits that affect the insect visitors capable of accessing these resources, and includes observations of visitors when these are available. References supporting statements about particular plant taxa are provided in Tables S1 and S2.

Grasses, the predominant herbaceous plants in the region, and sedges are not included in this study. They are anemophilous, that is adapted for wind-pollination. However, although (almost all) grasses do not produce nectar (Bernardello, 2007), their pollen is exploited by some insects, among them important pollinators including honeybees, halictid bees, and

Table 1. Flower types represented in the Sahel.

Flower types	Examples in Sahel	Characteristics	Pollinators (observed or suspected)	References
Nectarless, buzz-pollinated	<i>Commelina</i> (Commelinaceae), <i>Heteranthera</i> (Pontederiaceae), <i>Senna</i> , <i>Chamaecrista</i> (both Fabaceae) <i>Momordica</i> spp. (Cucurbitaceae)	Usually offer pollen only (some also offer nectar), porictidal anthers	Potentially half of all bee species (but not honeybees), ranging from carpenter bees to some Halictidae	Vallejo-Marin <i>et al.</i> (2010); De Luca & Vallejo-Marin (2013); Pritchard & Vallejo-Marin (2020)
Oil flowers		Oil, nectar, pollen	<i>Ctenoplectra</i> bees (Apidae)	Eardley <i>et al.</i> (2009); Renner & Schaefer (2010); but see Oronje <i>et al.</i> (2012a)
Carinate flowers	Fabaceae (Faboideae), Polygalaceae	Keel flowers, many with tripping mechanisms, explosive pollen release	Diverse bee species, varying in size, strength, and behavioural traits (e.g. large flowers of <i>Crotalaria retusa</i> are pollinated by relatively large carpenter bees; <i>Alysicarpus</i> and <i>Indigofera</i> are pollinated by diverse smaller bees (<i>Apis</i> , social and semi-social Halictidae)	Aygören Uluer <i>et al.</i> (2022)
Flowers with tubular corollas	Pedaliaceae, Rubiaceae, <i>Ipomoea</i> spp. (Convolvulaceae), others	Corolla tubes varying in length, restricting access (e.g. to long-tongued visitors) to varying degrees. Adaptation to diverse pollinators among species of <i>Ipomoea</i> , and also of <i>Kohautia</i> (Rubiaceae) to butterflies (red flowers of <i>K. senegalensis</i>) or settling moths (white flowers of <i>K. tenuis</i>)	Hymenoptera, Diptera, Lepidoptera, depending on flower characteristics	Hassa <i>et al.</i> (2023)
Hawkmoth flowers	Some <i>Ipomoea</i> spp. (Convolvulaceae), <i>Datura</i> (Solanaceae), <i>Pancratium</i> (Amaryllidaceae)	Large white flowers with trumpet-like tubular corollas, opening at night	Hawkmoths	Grant & Grant (1983); Willmott & Burquez (1996)
Settling moth flowers	<i>Kohautia tenuis</i> (Rubiaceae), <i>Dipcadi viride</i> , <i>Drimia indica</i> (both Asparagaceae)	Small, often pale-coloured inconspicuous flowers (usually white or green), strong nocturnal scents, and short nectar spurs, abundant nectar and sturdy structures to support the moths as they settle to feed	Settling moths (e.g. Geometridae, Noctuidae)	Groeninckx <i>et al.</i> (2010); Van Zandt <i>et al.</i> (2020)
Asclepiadoideae: morphologically specialised flowers, but great variation in pollination systems	<i>Leptadenia</i> spp., <i>Pergularia daemia</i> , <i>Calotropis procera</i>	Pollination requires detachment, transport and deposition of pollinia. Most species offer nectar as a reward, never pollen, occasionally nectarless.	Diverse pollinators (e.g. small Diptera, bees, wasps, depending on the species)	Ollerton <i>et al.</i> (2003, 2017, 2019)
Brood-site weevil pollination	<i>Annona senegalensis</i> (Annonaceae), <i>Ptilostigma</i> , <i>Vachellia</i> (both Fabaceae)	No unique morphological syndrome, widely divergent floral phenotypes	Curculionoidea (Coleoptera)	Dao <i>et al.</i> (2023); Haran <i>et al.</i> (2023)

(Continues on next page)

Table 1. (Cont.)

Flower types	Examples in Sahel	Characteristics	Pollinators (observed or suspected)	References
Ant pollination	<i>Euphorbia</i> (Euphorbiaceae), <i>Phyllanthus</i> (Phyllanthaceae)	Prostrate habit, frequent ant visits; small inconspicuous flowers, inflorescence-associated tiny nectaries	Ants	Sharma <i>et al.</i> (2009); Samuel & Rastogi (2022)
Deceit pollination	<i>Stylochaeon hypogaeus</i> (Araceae), <i>Cleome monophylla</i> (Cleomaceae)	Deceptive floral structures, mimicry, kettle-trap inflorescences, often conspicuous (when mimicry is visual)	Beetles attracted to rewardless kettle-trap inflorescences (<i>Stylochaeon</i>); fake nectaries reported for <i>Cleome monophylla</i> (requires confirmation)	Renner (2006); Lunau <i>et al.</i> (2017)

hoverflies (Bogdan, 1962; Immelman & Eardley, 2000), and Saunders (2018) speculates that many grasses may be pollinated by both wind and insects. Whether flower-visiting insects in arid savannas of the northern Sahel exploit grass pollen, and whether they are important in grass pollination, are questions that have not been explored.

Almost all of the Sahelian forbs listed possess flowers adapted for insect pollination (see Table S1). Exceptions are *Acalypha* spp. (Euphorbiaceae) and Amaranthaceae such as *Amaranthus* spp. and *Pandiaka angustifolia*. Wind-pollination is common in the latter family. As in grasses, pollen of wind-pollinated Amaranthaceae is collected by some bees. Such species may be ambophilous, that is pollinated both by insects and by wind (Abrahamczyk *et al.*, 2023). Finally, one species of Amaranthaceae in the region, *Aerva javanica*, is apomictic and pollination is not required for its reproduction.

Few studies of the floral biology of forbs have been conducted in the northern Sahel. Most have hermaphrodite flowers and many appear to be self-compatible (Table S1). Most trees, by contrast, are (largely) self-incompatible (Table S2). This reflects a general difference between these two growth forms, and is one of many that make seed production by trees more highly dependent on pollinators than is the case for herbs (Rodger *et al.*, 2021).

There are scattered observations of insect visitors of several widespread species from elsewhere in their range, but for most species we only have information on floral traits that affect their likely spectrum of visitors. Among animal-pollinated plants, there exists a continuum between extreme generalism (plants pollinated by up to hundreds of pollinator species) and extreme specialism (plants pollinated by a single pollinator species) (Johnson & Steiner, 2000). Descriptions of specialised floral traits have tended to associate frequent combinations of these traits with described pollination syndromes. However, there is much debate about the extent to which floral traits of plant species fall into discrete clusters in multivariate phenotype space that identify convergent syndromes, and about whether the most common or most effective pollinators of a plant can be predicted from the syndrome to which the plant is thought to belong (Ollerton *et al.*, 2009, 2015; Rosas-Guerrero *et al.*, 2014; Aguilar *et al.*, 2015; Amorim *et al.*, 2022). Pollination syndromes have been postulated for several plants included in this study, and we report this information where it has been given. However, we focus on flower types, rather than syndromes, to characterise the diversity of floral traits that restrict access to each plant's reproductive organs, floral rewards, or both, to visitors with appropriate morphology and behaviour (Table 1).

(2) Flower types represented in plants of Sahelian savannas

Many plants of Sahelian savannas have open, polypetalous, actinomorphic flowers, usually hermaphrodite, in which rewards (pollen, nectar, or both) and sexual organs are freely exposed to diverse insect visitors. Such flowers are expected

to be visited, and perhaps pollinated, by a broad spectrum of insects. Among forbs, examples of such open-access flowers in the northern Sahel include members of the families Aizoaceae, Asteraceae (compact inflorescences analogous to open-access flowers), Caryophyllaceae, Capparaceae, Geraniaceae, Malvaceae, Molluginaceae, Portulacaceae, Zygophyllaceae, and others. Most tree species in the northern Sahel also possess such flowers. Examples include Combretaceae, Fabaceae subfamily Mimosoideae (compact inflorescences analogous to open-access flowers), Rhamnaceae, and Zygophyllaceae. In all these families of forbs and trees, most species are known to possess floral nectaries (Bernardello, 2007). All appear to fit the notion of the “small diverse insects” (SDI) pollination system, recently reviewed by Moreira & Freitas (2020). The extreme generalism of their flowers, offering access to a broad range of visitors, may offer great advantages in these extreme environments, because “good years” for some insects may be “bad years” for others (Powell *et al.*, 2024). The flexibility of the SDI system is analogous to that provided by ambophily, and some SDI flowers may also be ambophilous. Many ambophilous species arose from SDI ancestors (Abrahamczyk *et al.*, 2023).

However, even among plants with generalist flowers, there is considerable variation in some floral traits and corresponding variation in their assemblages of insect visitors. Mimosoid legumes, which dominate the tree flora of the northern Sahel, provide such examples. The dense, many-flowered inflorescences of *Vachellia nilotica* and *V. tortilis* are visited by larger bees which avoid related mimosoid species with loose, few-flowered inflorescences. Also, some mimosoids offer only pollen as a reward (e.g. *V. nilotica*), while others, in addition to pollen, offer large (*Senegalia senegal* and *Faidherbia albida*) or small (*V. tortilis*) amounts of nectar (Tybirk, 1993; Stone *et al.*, 2003). These and other differences lead to different, but overlapping, assemblages of insects that visit co-occurring and co-flowering species (Stone, Willmer & Rowe, 1998). Species that offer both pollen and nectar tend to be visited by a greater diversity of insects (Stone *et al.*, 2003). Further study of the floral ecology of Sahelian plants with open-access, generalised flowers may reveal other examples of trait differences that lead each species to attract diverse, but only partially overlapping, sets of floral visitors.

In contrast to open-access flowers, those of other species have traits that restrict the range of flower visitors able to access rewards and reproductive organs. For species occurring in the Sahel, the information we have concerns almost exclusively morphological and phenological (e.g. day- or night-blooming) traits. Little information exists for other traits. For example, we are aware of no studies of floral odours in the region. The available information allows the categorisation of several flower types (Table 1). Across all species, pollen and nectar are the principal rewards offered to visitors. Oil flowers include only one genus [two species of *Momordica* (Cucurbitaceae)]. *Momordica* is also the only genus in the region reported to be associated with an insect strictly dependent on its flowers [*Ctenoplectra* (Apidae) bees].

A few species (in three families) offer only pollen as a reward, and depend on buzz-pollinating bees. Brood sites are provided as an attractant for a few weevil-pollinated tree species. Deceptive rewardless flowers are known for two species in the region. Among the species whose flowers have morphological structures that restrict access, the most important are the Faboideae, all of which have carinate (keel) flowers, pollinated by insects (usually bees) capable of releasing anthers [by tripping or other mechanisms (see Table S1)] from beneath the keel. Flowers with tubular corollas that restrict access are also frequent, and probably represent diverse pollination systems, including adaptations for pollination by Lepidoptera such as hawkmoths (both long- and short-tongued; Johnson *et al.*, 2017), settling moths, and butterflies (Table 1). Variation in floral traits among congeneric species of *Ipomoea* (Convolvulaceae) and *Kohautia* (Rubiaceae) suggests adaptation to different pollinators. An example of how little is known about pollination in this diverse group with tubular corollas is offered by *Adenium obesum* (Apocynaceae), the only succulent shrub common in the northern Sahel with long tubular corollas. Astonishingly, although the morphological adaptations of this common and widespread species for pollination by long-tongued insects were described in detail over 40 years ago (Rowley, 1980), we could find no published observations of its flower visitors from anywhere in Africa. Information is also lacking for the Sahel on pollination of Asclepiadoideae, whose morphologically specialised flowers represent a great diversity of pollination systems, from highly specialised to generalised. Among the most specialised systems are found in *Ceropegia*. Flowers of the around 180 species of this genus temporarily trap pollinators, usually small Diptera from one or more of 11 families. Many *Ceropegia* spp. are visited and pollinated by flies of only a single genus (Ollerton *et al.*, 2017). Judging from georeferenced observations in the Global Biodiversity Information Facility (GBIF), few species have been recorded in the northern Sahel (GBIF taxon ID: 7150518). Of the 17 West African species listed by Hutchinson *et al.* (2014), only one *Ceropegia* sp. (*C. aristolochioides*) appears to have been recorded from the northern Sahel, where it is rare (Meve *et al.*, 2001). Interestingly, this species, which we have not encountered in our fieldwork, interacts with and is pollinated by a larger range of flies than most *Ceropegia*: six families for the nominal subspecies in East Africa, at least 15 families for another subspecies in Arabia (Ollerton *et al.*, 2017). Finally, the suspected occurrence of ant pollination in two genera of prostrate herbs in the Sahel needs to be confirmed.

(3) Plant phenology

Species can only interact if their traits enable them to. In Section II.2 we considered the matching of morphological and behavioural traits between flowers and the insects that visit them. Phenological traits of plants and insects must also match. A match, or mismatch, between when flowers are available and when flower-visiting insects are active is essential in determining what interactions between flowering

plants and insects will occur. Phenology thus strongly affects the involvement of a plant species in insect–flower networks (Guzman, Chamberlain & Elle, 2021). In highly seasonal environments such as the northern Sahel, niche-based processes related to phenology can play major roles in shaping interaction networks (Vizentin-Bugoni *et al.*, 2018).

How does the availability of floral resources vary across seasons and between years? Sahelian ecosystems face strong abiotic constraints that shape the phenology of plant communities. In the Ferlo region of northern Senegal, rainfall is not only scarce, varying from 50 to 300 mm per year at a single site (Cissé *et al.*, 2016), but is also highly seasonal. Non-graminoid herbaceous annuals of the region, most of which are insect-pollinated, are thus limited to short vegetative and flowering seasons. Flowering seasons of perennial forbs [e.g. geophytes such as *Pancratium* (Amaryllidaceae), *Corallocarpus epigaeus* (Cucurbitaceae), *Dipcadi viride* and *Drimia indica* (both Asparagaceae)] may be somewhat less constrained, owing to their underground storage organs. In extreme northwestern Senegal, the bulb-bearing geophyte *Pancratium* sp. flowered much earlier than the other herbaceous plants, all of which were annuals and hemicryptophytes (Bille & Poupon, 1972). Flowering periods of other geophytes have not been described. In contrast to herbaceous plants, the perennial root systems of woody plants (shrubs, woody vines, but especially trees) should afford year-round access to groundwater, freeing their phenology from dependence on current rainfall. Woody plants thus have longer vegetative seasons and can flower during the dry season, potentially providing resources to floral visitors throughout the year. For the same reason, floral resources of woody plants are also likely to be less strongly affected by interannual variation in precipitation than those of forbs.

Two-thirds or more of the herbaceous species of the northern Sahelian savannas are annuals (Bille & Poupon, 1972; Breman & de Ridder, 1991). Studies of their phenology have concentrated on vegetative traits important to their role as forage resources, such as time of germination and phenology of growth. Little information is available about their reproductive phenology. All herbaceous plants in these savannas have short flowering periods restricted to the rainy season. Flowering begins in the early rainy season (July in the Ferlo of northern Senegal), but peaks near the end of the rains (October) (Bille & Poupon, 1972; Diatta *et al.*, 2023).

Trees of arid savannas have among the deepest roots known in any environment (Schenk & Jackson, 2005). For example, Do *et al.* (2008) found living roots of *Acacia* (now *Vachellia nilotica*) at 25 m depth. Rooting depth is a key trait shaping many aspects of the ecology of savanna trees (Zhou *et al.*, 2020), including their flowering phenology. Trees of arid environments also have greater capacity for water storage in stems, and trees such as baobab may use stem-stored water for flowering when soil water availability is low (Venter & Witkowski, 2019). Such traits explain how, in savannas that are among the driest in the world (Do *et al.*, 2008), “Whatever the month of the year, there are always [tree] species in bloom” (Poupon & Bille, 1974,

p. 61; our translation). Resources for flower-visiting insects provided by trees are thus available throughout the year (Table 2).

For the same reason, floral resources of woody plants are also less likely than those of forbs to be affected by the strong interannual variation in precipitation that characterises the northern Sahel (Do *et al.*, 2008). Shrubs, which are smaller than trees, also have significantly shallower maximum root depths than trees in similar environments (Schenk & Jackson, 2002). Shrubs that continue vegetative activity, reproductive activity, or both, during the dry season may thus be restricted to topographic depressions where the water table is relatively shallow. These low-lying sites are of crucial importance in conserving plant diversity in the northern Sahel (Dendoncker & Vincke, 2020; Dendoncker *et al.*, 2023).

As elsewhere in African savannas (e.g. Ryan *et al.*, 2017), tree species of the northern Sahel exhibit diverse flowering phenologies. Leafing and flowering are not independent events, but are linked developmentally and physiologically (van Schaik, Terborgh & Wright, 1993). For example, leaf shedding can trigger flowering as a result of stem rehydration (Singh & Kushwaha, 2006). Leafing phenology is clearly of adaptive significance in Sahelian savannas. To understand the extent to which the floral phenology of Sahelian trees is driven by selection on leafing phenology, it is important first to understand the proximate mechanisms determining leafing phenology in Sahelian trees, and the selective pressures driving it.

Phenological data for the dry tropics are sparse, and the processes controlling leaf emergence are not well understood (Richardson *et al.*, 2013). Leafing phenology is related to climate patterns in the Sahel, but the relationship is not simple. Hiernaux *et al.* (1994) identified five phenological types among Sahelian trees (Table 3). In all of these, flowering precedes or coincides with leafing out. In trees with variable leafing phenology, flowering phenology is just as variable. In some evergreen species, however (e.g. *Combretum glutinosum*), there is no obvious relationship between leafing and flowering (Seghier *et al.*, 2012a). According to Coulibaly *et al.* (2020), *Combretum glutinosum* and other Combretaceae of the region are characterised by longer flowering seasons than most other trees in West African savannas.

Trees in type 4 (Table 3) leaf out and flower well before the rains. Such “pre-rain green-up”, permitted by the deep roots of savanna trees and by their capacity to use stored reserves, is widespread in African savannas, where many trees leaf out and flower often several weeks before the onset of rains (Ryan *et al.*, 2017). A consequence is that flowers of such trees offer energy and water (and pollen for some visitors) near the end of the dry season, a period when these resources might otherwise be scarce. The costs and benefits of pre-rain green-up as a vegetative strategy are discussed by Ryan *et al.* (2017) and Stock (2017). The costs and benefits of precocious flowering have been less discussed.

We found no information on how flowering phenology in plants of the northern Sahel responds to the considerable inter-annual variation in rainfall that characterises the region. However, as in the case of seasonal variation, forbs,

Table 2. Seasonal patterns in flowering phenology of Sahelian tree species (Arbonnier, 2000). [Correction added on 30 November 2024, after first online publication: Shading in Table 2 has been amended.]

Tree and shrub species	Dry season (1st half)	Dry season (2nd half)	Rainy season (1st half)	Rainy season (2nd half)
<i>Calotropis procera</i> (Aiton) Aiton	Shaded	Shaded	Shaded	Shaded
<i>Guiera senegalensis</i> J.F.Gmel.	Shaded	Shaded	Shaded	Shaded
<i>Balanites aegyptiaca</i> (L.) Delile	Shaded	Shaded	Shaded	Shaded
<i>Adansonia digitata</i> L.	Shaded	Shaded	Shaded	Shaded
<i>Adenium obesum</i> (Forssk.) Roem. & Schult.	Shaded	Shaded	Shaded	Shaded
<i>Commiphora africana</i> Engl.	Shaded	Shaded	Shaded	Shaded
<i>Boscia senegalensis</i> Lam.	Shaded	Shaded	Shaded	Shaded
<i>Boscia integrifolia</i> J.St.-Hil (syn: <i>Boscia angustifolia</i> A.Rich.)	Shaded	Shaded	Shaded	Shaded
<i>Combretum nigricans</i> Lepr. ex Guill. & Perr.	Shaded	Shaded	Shaded	Shaded
<i>Faidherbia albida</i> (Delile) A.Chev.	Shaded	Shaded	Shaded	Shaded
<i>Leptadenia hastata</i> Vatcke	Shaded	Shaded	Shaded	Shaded
<i>Combretum aculeatum</i> Vent.	Shaded	Shaded	Shaded	Shaded
<i>Vachellia seyal</i> (Delile) P.J.H.Hurter	Shaded	Shaded	Shaded	Shaded
<i>Leptadenia pyrotechnica</i> (Forssk.) Decne.	Shaded	Shaded	Shaded	Shaded
<i>Terminalia avicennioides</i> Guill. & Perr.	Shaded	Shaded	Shaded	Shaded
<i>Combretum glutinosum</i> Perr. ex DC.	Shaded	Shaded	Shaded	Shaded
<i>Combretum micranthum</i> G.Don	Shaded	Shaded	Shaded	Shaded
<i>Tamarindus indica</i> L.	Shaded	Shaded	Shaded	Shaded
<i>Dalbergia melanoxylon</i> Guill. & Perr.	Shaded	Shaded	Shaded	Shaded
<i>Dichrostachys cinerea</i> (L.) Wight & Arn.	Shaded	Shaded	Shaded	Shaded
<i>Vachellia nilotica</i> (L.) P.J.H.Hurter & Mabb.	Shaded	Shaded	Shaded	Shaded
<i>Sterculia setigera</i> Delile	Shaded	Shaded	Shaded	Shaded
<i>Senegalia senegal</i> (L.) Britton (syn: <i>Acacia senegal</i>)	Shaded	Shaded	Shaded	Shaded
<i>Pterocarpus lucens</i> Lepr. ex Guill. & Perr.	Shaded	Shaded	Shaded	Shaded
<i>Vachellia tortilis</i> subsp. <i>raddiana</i> (Savi) Kyal. & Boatwr.	Shaded	Shaded	Shaded	Shaded
<i>Grewia damine</i> Gaertn. (syn: <i>Grewia bicolor</i> Juss.)	Shaded	Shaded	Shaded	Shaded
<i>Ziziphus mauritiana</i> Lam.	Shaded	Shaded	Shaded	Shaded

Table 3. Phenological types of Sahelian tree species (Hiernaux *et al.*, 1994).

Phenological type	Example species
(1) Deciduous trees with short-lived leaves	<i>Commiphora africana</i> , <i>Capparis decidua</i>
(2) Deciduous trees with long-lived leaves	<i>Vachellia tortilis</i> , <i>Combretum aculeatum</i>
(3) Deciduous trees with variable leafing phenology	<i>Balanites aegyptiaca</i> , <i>Ziziphus mauritanus</i>
(4) Pre-rainy season evergreens	<i>Ptilostigma reticulatum</i> , <i>Combretum glutinosum</i>
(5) Post-rainy season evergreens	<i>Boscia senegalensis</i> , <i>Bauhinia rufescens</i>

particularly the annual species that predominate in the region, are expected to be much more sensitive to inter-annual variation than are trees (Wright *et al.*, 2015). The composition of annual species, both grasses and forbs, is completely determined by the dynamics of their soil seed

banks. Seeds of most annual grasses of the northern Sahel germinate rapidly early in the rainy season, whereas seeds of most forbs germinate slowly, and may fail to germinate in large numbers in very dry years. The relative success of these two germination strategies varies in complex ways both in space, in response to variation in soil type, degree of shade, litter accumulation, and grazing pressure, and in time, with variation among years in total rainfall and its temporal patterning (Breman & de Ridder, 1991). The abundance of forbs (and thus of resources for flower-visiting insects) and their species composition are both likely to show correspondingly great variation in space and among years.

There are many open questions about the phenology of floral resources in the Sahel. First, information on diel cycles in the production of floral resources in northern Sahelian savannas has never been synthesised; only scattered information exists for particular species. Some forbs are night-blooming, in keeping with observed (e.g. *Pancratium*; Manning & Smith, 2017) or expected (e.g. *Datura metel*; Table 1) pollination by moths. The most detailed studies on

diel cycles in production of floral resources – conducted elsewhere in Africa but including species found in the Sahel – are those of Stone, Willmer & Nee (1996) and Stone *et al.* (1998) on *Acacia* spp. (including *Vachellia* and *Senegalia*). As emphasised by Stone *et al.* (1996), community data sets consistently show varying degrees of flowering season overlap, particularly in arid environments where flowering season may be constrained by climate. When such co-flowering species share pollinators, diurnal separation of flowering times minimises this overlap, allowing temporal partitioning of pollinators. This temporal separation could transform interspecific competition into facilitation, in which the floral resources provided by several species combine to maintain their shared pollinators. Stone *et al.* (1998) showed that sympatric co-flowering African *Acacia* spp. exhibited high intraspecific synchrony in pollen release, but that different species released their pollen at different times of day. Such temporal separation between related species reduces both interspecific competition and the risk of interspecific pollen transfer and hybridisation.

Similarly, there is only scattered information on longevity of individual flowers. Those of *Commelina* spp., known as day-flowers, typically last less than one day, but opening times during the day vary among species (Faden, 2000). Flowers of *Citrullus colocynthis* are reported to open early in the morning and also last only one day (Kuti & Rovelov, 1992).

III. STATE OF KNOWLEDGE ABOUT THE FAUNA OF FLOWER-VISITING AND POLLINATING INSECTS IN SAHELIAN SAVANNAS

(1) Hymenoptera

Bees (Anthophila) are the most important pollinators in most ecosystems. Both social and solitary bees are completely

dependent on floral resources throughout their life cycle. In contrast to most flower-visiting insects, bees seek primarily pollen and not only nectar, and thus act not only as pollinators but also as herbivores, whose consumption of pollen does not benefit the plant. Plants have thus evolved diverse strategies to protect pollen and maximise its transfer to conspecific stigmas, and bees have developed strategies to counter these and efficiently exploit pollen. This interplay of strategies is an important dimension of specialisation in bee–flower interactions (Praz, 2008). Bees differ in their ecological requirements, and thus in their ecogeographic distribution. Tropical grasslands, especially drylands like the northern Sahel, are dominated by solitary bees. Around three-quarters of solitary bee species are ground-nesting (Antoine & Forrest, 2021). The much lower prevalence of fungal or other pathogens that could destroy brood or nest provisions probably contributes to the greater frequency of ground-nesting in arid environments compared to the humid tropics (Michener, 1979; Winfree, 2010). In warm-temperate dry environments, most solitary bee species have short activity periods (sometimes only a few weeks), with usually a single generation per year and extended adult, prepupal or larval diapause (Danforth, Minckley & Neff, 2019). Different species have short, overlapping flight periods, and the impossibility of seasonal segregation may favour specialisation on one or a few related pollen hosts. However, in dry tropical grasslands such as the northern Sahel, polylectic species predominate, and life cycles have not been studied (see Table 4). The short duration of forb flowering periods, the greater unpredictability of forb flowering across years, and the availability of tree flowers throughout the year, may all favour polylectic species, with longer-lived adults or with multiple generations per year.

There are important fundamental gaps in our knowledge of bee biology (Winfree, 2010). For tropical Africa, whose

Table 4. Characteristics of bee communities in tropical grasslands compared to warm-temperate dry environments.

Bee community	Characteristics	Nesting habits and life cycles	Prevalence of specialists	Flowering phenology
Tropical grasslands, including the northern Sahel	Dominated by solitary bees; predominantly polylectic species. Bee fauna less diverse compared to warm-temperate dry environments	Most are ground-nesting; solitary bees usually have short-lived adults with single generation per year (some species with extended diapause), but life cycles of Sahelian species apparently unknown	Predominantly polylectic species; few pollen specialists recorded (<i>Ctenoplectra</i> spp. (Apidae), <i>Systropha</i> spp. (Halictidae))	Short flowering periods of forbs, great inter-annual climatic variation, and availability of tree flowers throughout the year favour polylectic species
Warm-temperate dry environments	Dominated by solitary bees; richer bee fauna than tropical grasslands; presence of oligolectic species; in most xeric areas, flowering of forbs and bee flight seasons tend to be synchronised on favourable seasons	Ground-nesting; short-lived adults with single generation per year; overlapping flight periods	Presence of both polylectic and oligolectic species	Long flowering periods; cold limits insect activity during winter

bee fauna is poorly studied relative to those of other regions, these gaps are even larger. The depauperate nature of the African bee fauna compared to that of other tropical regions (Michener, 1979) may be more apparent than real, as there are probably many undescribed species (Eardley, Gikungu & Schwarz, 2009). The gaps concern not only species richness, but also basic information on biology, even for common bee species. Apart from a few cases discussed in Section II.2 – bees visiting oil flowers, keel flowers, and buzz-pollinated flowers – little is known about bee and flower traits that may constrain interactions between particular species. To the best of our knowledge, there are no multi-year studies monitoring populations of any bee over time in the northern Sahel. Little appears to be known about the lifespan, fecundity, and seasonal and annual life cycles of bee species in the region. Interestingly, bivoltine or multivoltine life cycles are more frequent in Halictidae, which are diverse in the Sahel, than in other solitary bees (Danforth *et al.*, 2019). The question of what factors limit bee populations is globally little explored, and completely unexplored in the Sahel.

Three other groups of Hymenoptera – aculeate wasps (sphecoids and vespoids), hymenopteran parasitoids, and ants – frequently visit flowers and are well represented in Sahelian savannas. Unlike bees, these insects (with the exception of masarine pollen wasps; see Table 5) depend on flowers for only part of their food. Aculeate wasps – that is those with stings – are well represented and abundant in the Sahel. Some solitary wasps are prey specialists (e.g. Pompilidae feed only on spiders), while others (e.g. Crabronidae) feed on a vast diversity of prey. Social wasps are opportunistic generalist predators (Table 5). Like aculeate wasps, hymenopteran parasitoids are extremely diverse and frequent floral visitors in the northern Sahel. Predatory and parasitoid wasps use nectar to fuel their search for prey and hosts, respectively. Ants are also frequent flower visitors. They may play a role in pollination of a few prostrate herbs in the Sahel, but otherwise their roles in floral ecology are indirect (preying on florivores, dissuading pollinators).

(2) Diptera

Diptera are usually considered the second most important group of pollinators (Ollerton, 2017). Africa harbours a rich dipteran fauna, and the savannas have a much greater species richness than the rainforest regions (Kirk-Spriggs & Stuckenberg, 2010). A three-volume treatise edited by Kirk-Spriggs & Sinclair (2017–2021) provides a wealth of information on Afrotropical Diptera. The hairy bodies of many Diptera make them effective pollen transporters (Cook *et al.*, 2020). Larson, Kevan & Inouye (2001) list 55 families that include flower-visiting species. Among the most important are Bombyliidae and Syrphidae, both well represented in Sahelian savannas. Many Bombyliidae are “major pollinators of arid-area flowering plants, especially annuals” (Evenhuis & Lamas, 2017, p. 1020). Afrotropical

representatives of these families occur mainly in semi-arid and arid regions (Banda *et al.*, 2020). The high mobility of hoverflies should enable them to effect pollen transport in plant species occurring at low densities or in fragmented habitats (Doyle *et al.*, 2020). However, this has not been studied in Afrotropical syrphids.

Like hymenopteran predators and parasitoids, many flower-visiting flies use nectar to fuel their search for larval hosts or prey. Davis *et al.* (2023) present extensive data on diet and habitats of both larval and adult stages of pollinating Diptera. While many short-tongued Diptera visit open-access flowers, several families, including Syrphidae, Bombyliidae, Tabanidae, and others, have long-tongued members that can exploit nectar in long-tubular corollas (Krenn, Plant & Szucsich, 2005). Like predatory and parasitic Hymenoptera, flower-visiting Diptera perform numerous ecosystem functions in addition to pollination (e.g. regulation of host and prey populations; decomposition), and their frequent position at high trophic levels makes them good indicators of the continued presence of the diverse organisms comprising the food webs on which they depend (see Table 6).

Among the numerous other fly families that include highly effective pollinators are the Calliphoridae (blow flies) and Tabanidae (horse and deer flies), two families with important impacts on the health of humans and animals, particularly in pastoralist economies.

(3) Lepidoptera

Lepidoptera are frequent floral visitors and pollinators. Ollerton (2017) considered this order the most diverse of all groups of insect pollinators, owing to the undoubtedly large number of – mostly unstudied – flower-visiting moths. Larvae of almost all butterflies and moths are phytophagous, and it is not surprising that their diversity generally follows latitudinal gradients of plant diversity and productivity (Delabye *et al.*, 2022; Pinkert *et al.*, 2022). We found no studies of butterfly or moth pollination in the northern Sahel, but the three moth families most frequently cited as pollinators elsewhere – Sphingidae, Noctuidae, and Geometridae (Table 7) – are all well represented. Among butterflies, Pieridae and Lycaenidae are particularly abundant, and the region’s butterfly fauna includes one famous long-distance migrant, the Painted Lady (Nymphalidae) (see Table 7).

(4) Coleoptera

Beetles of over 30 families have been observed to visit flowers (Muinde & Katumo, 2024). Although beetle-pollination systems were long thought to be relatively inefficient, Coleoptera are now considered to be fourth among insect orders in importance as pollinators, and second in importance, after Hymenoptera, in tropical ecosystems (Muinde & Katumo, 2024). Among the most significant are the flower beetles, or flower chafers (Scarabaeidae: Cetoniinae) (Ollerton, 2017). Numerous weevil species (Curculionoidea) are involved in specific brood-site pollination mutualisms with various tropical trees, and some of these occur in the Sahel (Table 8).

Table 5. Characteristics of hymenopteran flower visitors.

Hymenopteran group	Characteristics	Importance in pollination	References
Halictidae	Short-tongued bees; diverse; may include cryptic species; most oligolectic African species are from Mediterranean north Africa and South Africa	Critical pollinators, they pollinate a variety of plants; high diversity of morphologically similar species. The nine species of <i>Systropha</i> encountered in the Afrotropics (the only known oligolects in the region) are frequently collected in flowers of Convolvulaceae. Several species of this plant family are abundant in the Sahel but their pollination is unstudied	Michener (1979); Pauly (1984); Patiny <i>et al.</i> (2007); Danforth <i>et al.</i> (2008); Eardley <i>et al.</i> (2010)
Megachilidae, <i>Xylocopa</i> spp.	Long-tongued	Critical pollinators, they exploit nectar and pollen hidden in structures such as long-tubular corollas	Alexander & Michener (1995)
Aculeate wasps (sphecoids and vespoids)	Abundant in the Sahel; solitary predators (97%) or parasites of other arthropods; floral nectar fuels their search for prey. Viewed as nuisances, the value of the ecosystem services they provide is widely overlooked	Generalists; specific contributions to pollination effectiveness are not extensively studied	Brock <i>et al.</i> (2021)
Masarinae (Vespidae)	Solitary wasps adopting feeding habits similar to bees; provision larvae with pollen and nectar; only three Masarinae species have been recorded from West Africa. Documented cases of obligate pollination by specific species.	May contribute to pollination, especially in cases of specific plant associations. Poorly represented in the Sahel	Gess (1992); Carpenter (2001); Gess & Gess (2004)
Ichneumonoidea, Chalcidoidea	Two hyperdiverse superfamilies (for Chalcidoidea, estimates of more than 500,000 species); use nectar for energy to search for hosts, as well as other plant-derived foods (e.g. honeydew). Complex host-specific interactions; role in controlling arthropod populations	Limited information about their role as pollinators; generalist and frequent flower visitors; lack of comprehensive studies on parasitoid–flower interactions	Jervis <i>et al.</i> (1993); Smith <i>et al.</i> (2008); Menz <i>et al.</i> (2015); Zemenick <i>et al.</i> (2019); Cruaud <i>et al.</i> (2024); Polaszek & Vilhelsen (2023)
Ants	Frequently visit flowers, where they play diverse roles. Some species exploit floral resources; presence may enhance or reduce pollination services depending on interactions with other floral visitors	Pollinators of a few plant species (e.g. <i>Euphorbia</i> spp., <i>Phyllanthus</i> spp.); may enhance pollination services in some plant species by causing pollinators to make shorter visits and move more frequently between plants	Altshuler (1999); Romero & Vasconcellos-Neto (2004); De Vega & Gómez (2014); Rostás <i>et al.</i> (2018)

(5) Insect phenology in the harsh, variable, and highly seasonal climates of the Sahel

Like the phenological traits of plants, those of insects, assessed in relation to seasonal and diel cycles and inter-annual variation, influence the roles they can play in insect–flower networks.

Patterns of seasonality in insect activity in the seasonally dry tropics are extremely diverse. For each species, detailed data on its complete life cycle are required to understand its seasonal patterns, but 35 years after the seminal study by Wolda (1988), such data are still limited. In many species,

resources for immature stages are seasonally limited. For example, among flower-visiting insects, many dipteran families, including some Syrphidae, have aquatic larvae (Wagner *et al.*, 2008) and reproduce strictly in the rainy season. Similarly, insects whose immature stages depend on young growth of plants (or are parasites or predators of phytophagous insects) also have highly seasonal reproduction, often restricted to small fractions of the growing season. For example, parasitoids that attack different host stages (larvae, pupae) emerge earlier or later, respectively, in the growing season (Hopkins, Roininen & Sääksjärvi, 2019). After their

Table 6. Characteristics of dipteran flower visitors.

Dipteran group	Principal families	Characteristics	Importance in pollination	References
	Syrphidae (hoverflies)	Adults feed on nectar and pollen, require pollen for ovarian development. Some long-tongued species can exploit deep-tubular flowers; not restricted to a limited home range and may carry pollen over longer distances than bees	Highly effective pollinators, generalist visitors of many flower species, show floral consistency at the individual level	Larson <i>et al.</i> (2001); Doyle <i>et al.</i> (2020)
	Bombyliidae (beeflies)	Adults feed on nectar and pollen. Elongate proboscides enable them to feed on concealed nectar; some species feed on keeled flowers of faboid legumes but do not trigger the pollen-release mechanism	Highly effective pollinators, generalist visitors of many flower species	Kastinger & Weber (2001); Evenhuis & Lamas (2017)
	Nemestrinidae	Important pollinators in arid and semi-arid regions	Significant contributors to pollination, especially in regions with low rainfall	Banda <i>et al.</i> (2020)
Muscoidea	Calliphoridae, Anthomyiidae, Muscidae (common housefly)	Various species feed on nectar and pollen	Provide pollination services	Cook <i>et al.</i> (2020)
Various families of small flies	Mythicomyiidae, Chloropidae, Phoridae, Milichiidae	Diverse but poorly sampled; nectar and pollen of trees appear to be key resources for these and many other savanna Diptera	The role of Diptera as pollinators of flowering trees is likely underestimated in Africa	Kirk-Spriggs & Muller (2017)

Table 7. Characteristics of lepidopteran flower visitors.

Lepidopteran group	Characteristics	Importance in pollination	References
Sphingidae	Hawkmoths, hovering moths with varying proboscis lengths	Key pollinators in tropical and warm temperate regions; some species have long tongues for deep-reward flowers (Johnson & Raguso, 2016). They have been observed feeding on <i>Adansonia digitata</i> (Malvaceae) in South Africa, <i>Pancreatium tenuifolium</i> (Amaryllidaceae) and other Sahelian forb species, including <i>Ipomoea</i> (Convolvulaceae) and <i>Datura</i> (Solanaceae)	Ballesteros-Mejia <i>et al.</i> (2013); Johnson & Raguso (2016); Delabye <i>et al.</i> (2022); Karimi <i>et al.</i> (2022)
Noctuidae, Geometridae	Settling moths with shorter tongues	Rely on floral nectar as a food source. Plants likely visited include <i>Kohautia tenuis</i> (Rubiaceae), <i>Dipcadi</i> spp., <i>Drimia</i> spp. (both Asparagaceae)	Axmacher <i>et al.</i> (2009); Hahn & Brühl (2016); Hurme <i>et al.</i> (2022)
Pieridae	Abundant and diverse in Sahelian savannas. Larval hosts include Capparaceae (e.g. <i>Boscia</i>) and related plants	Known for long-distance migration	Cosson <i>et al.</i> (1996)
Nymphalidae	Includes the Painted Lady (<i>Vanessa cardui</i>), known for long-distance migrations. It has among the widest known larval-host ranges of any butterfly. <i>Zornia glochidiata</i> noted as a host in Senegal	Painted Lady migrates annually from West Africa to Europe, multiple generations per year during seasonal ranges	Hu <i>et al.</i> (2021); Talavera <i>et al.</i> (2023)
Lycaenidae	Abundant in Sahelian savannas, includes <i>Chilades eleusis</i> . Seasonal polymorphism has been recorded in some Indian species of this genus	Shorter proboscis and smaller bodies than Nymphalidae, Pieridae, Papilionidae, and Hesperidae; restricted to flowers with shorter corolla tubes. Known to feed on Asteraceae flowers in open grasslands	Larsen (2005); Staude <i>et al.</i> (2020)

Table 8. Characteristics of coleopteran flower visitors.

Coleopteran group	Characteristics	Importance in pollination	References
Scarabaeidae: Cetoniinae	Flower beetles are important pollinators; some are destructive herbivores of fruits and flowers; Afrotropical region has the greatest number of endemic genera of cetoniines. Larvae feed on decaying plant material, contributing to nutrient cycling; detailed ecology of African species largely unknown	More effective in transporting outcross pollen than widely believed. Often visit generalist flowers, but some plants have specific adaptations for pollination by cetoniines	Ollerton <i>et al.</i> (2003); Matsuki <i>et al.</i> (2008); Mudge <i>et al.</i> (2012); Touroult & Le Gall (2013); Mitchell <i>et al.</i> (2020)
Curculionoidea	Many involved in specialised brood-site pollination mutualisms with plants of various families; larvae often develop within plant tissues, contributing to nutrient cycling	Important pollinators of a few tree species in the Sahel. They are flower visitors of <i>Annona senegalensis</i> (Annonaceae), <i>Piliostigma reticulatum</i> (Fabaceae)	Dao <i>et al.</i> (2023); Haran <i>et al.</i> (2023)

short breeding season, these insects pass the dry season in a dormant state, as diapausing eggs, larvae, or pupae. Other parasitoids are polyphagous, using a succession of hosts and breeding through a longer period of the year (Kabore *et al.*, 2017). If adult resources continue to be available, insects may remain active, spending the dry season as adults in reproductive diapause. However, surviving a tropical dry season, particularly while remaining active, is much costlier energetically than surviving a temperate-zone winter (Denlinger, 2023). Floral nectar – which in the Sahelian dry season is produced only by trees and shrubs – may represent a key resource that allows dry-season activity of many insects. Floral nectar also supplies another crucial resource, water (e.g. Benoit *et al.*, 2023). A few insect species may even be able to reproduce year-round, even in the strongly seasonal climates of the northern Sahel. For example, both immature and adult stages of bees depend on nectar and pollen, and if at least some flowers are available, generalist bees might be able to breed year-round. Solitary bees vary, both within and among species, in their strategies of diapause and life history, with some tropical species not undergoing diapause (Santos, Arias & Kapheim, 2019). Whether some solitary bee species of the northern Sahel are active year-round is apparently unknown.

Signals and proximate mechanisms underlying dormancy and emergence from dormancy are not well understood in tropical insects, where temperature and photoperiod are less seasonally variable than in temperate environments. The timing of rainfall and its spatial patchiness in the seasonally dry tropics is often unpredictable (Denlinger, 2023). This may constrain the evolution of dormancy mechanisms and favour dispersal or migratory behaviour as an adaptation to seasonality (Jones, 1987). Thus, despite its costs, remaining active in the adult stage has important advantages, among them the ability to disperse opportunistically to new sites when favourable conditions reappear (Wolda, 1988).

Seasonal insect migrations are widespread, and have important consequences for pollination, as well as many other

ecosystem processes (Satterfield *et al.*, 2020). Long-distance migration appears to be an important component of the adaptation of Sahelian insects to seasonality. Borne by favourable southerly winds, huge numbers of insects of at least 100 families of 13 orders migrate from southern source regions into the Sahel each wet season, most of which make a return migration (again with favourable winds) at the end of the rainy season (Florio *et al.*, 2020). Migrants include representatives of numerous families with species known to visit flowers.

Beyond the importance of migration for many species, little is known about the seasonal phenology of arthropod communities in the northern Sahel. Working in the southern Sahel in western Senegal, Lingbeek *et al.* (2017) found that arthropod species richness was greater in the rainy season for all habitat types studied. However, arthropod taxa differed in their responses to seasonality. Whereas beetle richness was greater in the rainy season, richness of spiders and ants, two other diverse taxa represented by large numbers of morphospecies, was not significantly different between rainy and dry seasons. The structure of arthropod assemblages varied among seasons, and among habitat types. The effects of seasonality on assemblages of flower-visiting insects in the northern Sahel are expected to be highly variable across taxonomic and functional categories of insects. Insects whose immature stages depend on young vegetative growth, for example, may show stronger seasonality. By contrast, insects whose food resources supply water even in the dry season – for example predators such as ants – may be less affected by seasonal variation in rainfall. Similarly, nectar exploited by insects that visit flowers of trees may confer greater independence from current rainfall, enabling them to remain active during the dry season.

IV. NETWORK STRUCTURE AND FUNCTION

Recognising threats to biodiversity and the ecosystem functions it provides, as well as monitoring and managing these

threats, begins with an understanding of how each of the multiple plant and animal actors is linked to the others.

Analysis of the structure and dynamics of interaction networks is thus key to the nexus of biodiversity and restoration ecology (Kaiser-Bunbury *et al.*, 2017). Whether networks are robust to changes in species composition or are resilient, maintaining their functioning in the face of environmental changes, remains unknown for networks of flowers and flower-visiting insects in the northern Sahel. In fact, in Africa as a whole few studies of these interactions have applied a network approach (Vizentin-Bugoni *et al.*, 2018; for a recent example, see Dzekashu *et al.*, 2023), and we know of only one from sub-Saharan West Africa, in Sudanian savannas in Burkina Faso (Stein *et al.*, 2020).

What does the information presented above on traits of flowers and of the insects that visit them suggest about the structure and functioning of insect–flower networks in the northern Sahel?

First, the high proportion of species with open-access, generalist flowers, visited by diverse insects, suggests that morphological mismatches between flowers and insects may not constrain interactions to as great an extent as in many other tropical pollination networks (Vizentin-Bugoni *et al.*, 2018). Plant–pollinator networks tend to feature predominantly nested architecture in which interactions of specialist species are included within those of a densely connected core of generalist species in a hierarchical structure (Bascompte *et al.*, 2003). By contrast, modular networks feature subsets of species that preferentially interact with one another (Olesen *et al.*, 2007). The present evidence suggests that few such modules of interacting specialists are evident in the Sahel, compared with networks studied elsewhere in the tropics. A nested structure makes networks more resilient (Thébault & Fontaine, 2010), and the core of generalists plays a key role. Where generalists predominate, some sets of species may be functionally redundant, allowing persistence of network dynamics if some species are lost (Biggs *et al.*, 2020). Also, seed production tends to be less impacted by reduced pollination services in plants with generalised pollination systems than in those with specialised pollination systems, making the former less vulnerable to variation in pollinator availability (Rodger *et al.*, 2021).

Second, the phenology of plants and of pollinators critically affects their roles in networks (Encinas-Viso, Revilla & Etienne, 2012; Guzman *et al.*, 2021). Given the marked seasonality of the Sahel, spatio-temporal non-overlap probably greatly limits the proportion of all potentially possible interactions that actually occur. Insect species with a long period of activity can potentially interact with a larger number of plant species (e.g. De Manincor *et al.*, 2020). However, little information exists on the duration of flight seasons of flower-visiting insects in the Sahel. Likewise, plant species with long flowering seasons can potentially interact with a larger number of insect species. Trees have longer individual flowering seasons than forbs, and some tree species have longer flowering periods than others (e.g. Combretaceae; Coulibaly *et al.*, 2020). Given their open-access flowers, their longer individual flowering seasons, and the fact that they

collectively offer floral resources throughout the year, trees are likely to interact with a greater diversity of insects than do forbs. They are also a more reliable resource, as their flowering is less affected by inter-annual climatic variation than that of forbs (Wright *et al.*, 2015). As central nodes in networks, connected to many other species, they may be keystone species, whose disappearance would have a disproportionate effect on network persistence. Two kinds of centrality have been identified, and these appear to reflect different ways in which species act as keystones (Martín-González, Dalsgaard & Olesen, 2010). Closeness centrality (CC) of a node (species) measures its proximity to other nodes in the network. Species with high CC have the potential to affect many other species. Betweenness centrality (BC) identifies nodes that connect different parts of the network that otherwise would not be connected. In the northern Sahel, strong seasonality could lead to distinct seasonal sub-networks of flower-visiting insects. If this is so, trees may play an important role in connecting them.

Third, the surprisingly high diversity of flower-visiting insects in the northern Sahel (N. Medina-Serrano, A.-G. Bagnères, M. M. Ndiaye, V. Vrecko, D. McKey & M. Hossaert-McKey, in preparation) could increase the robustness of insect–flower networks, buffering them against the loss of individual species. Such “biodiversity insurance” could be particularly important in buffering against temporal variation in network functioning owing to phenological shifts caused by climatic fluctuation or climate change (Bartomeus *et al.*, 2013).

The apparent predominance of generalist plants that attract a diversity of flower-visiting insects, and the likely role of trees as connectors, represent sources of resilience in insect–flower networks in the northern Sahel. However, there is also potential network fragility. Whereas each tree species interacts with a large number of insect visitors, each insect visitor interacts with only a small number of tree species. Such asymmetry is a general feature of plant–pollinator networks. Consequently, removal of a plant species from the network is more likely to destabilise interactions than removal of an insect species (Jordano, Bascompte & Olesen, 2006). In the northern Sahel, where a few abundant tree species support a diverse fauna of flower-visiting insects, this asymmetry is particularly extreme. Consequently, the stability of networks may hinge on the floral resources provided by a small number of tree species during crucial periods. Failure of a crucial hub to flower in an unfavourable year therefore could have far-reaching consequences (*cf.* Erenler, Gillman & Ollerton, 2020).

To summarise, traits of both flowers and insects suggest networks featuring greater levels of generalism than in most pollination networks, indicating higher functional redundancy and hence greater robustness. As noted above, such opportunistic strategies of both flowering plants and flower-visiting insects may offer great advantages in dry, variable, and unpredictable environments. To our knowledge, only one study (Devoto, Medan & Montaldo, 2005) has attempted to test the hypothesis that generalism of flower visitors varies over a precipitation gradient.

However, their temperate-zone study covered a gradient from forest to shrub-grassland steppe, and even the driest site (mean annual rainfall 700 mm) was much wetter than the northern Sahel.

V. OPEN QUESTIONS AND RESEARCH PRIORITIES

(1) Structure and functioning of insect–flower networks and the impact of climate fluctuation and climate change

Our knowledge of the relationships between plants and their pollinators is far from complete (Ollerton, 2021), and even less is known about insect–flower interaction networks in the northern Sahel than in most parts of the world. Trees are likely crucial to the resilience of networks in the northern Sahel, due to their flowering extending over the year and to their great diversity of insect visitors (e.g. Tybirk, 1993; Stone *et al.*, 2003). However, it is not known whether some species are particularly important as keystone links or whether, on the contrary, trees collectively support diverse flower visitors. For forbs, information on insects visiting their flowers is completely lacking. Are they visited by a distinct set of species active only during the brief rainy season, or by species that also visit trees during all periods of the year? Information on nocturnal flower-visiting insects is also completely lacking. The hordes of insects present during rainy-season nights in the Ferlo make night-time sampling uncomfortable, but they also promise a rich assemblage of nocturnal flower visitors.

Phenological data are crucial for guiding and monitoring restoration actions (Buisson *et al.*, 2017). How does flowering phenology vary, seasonally and across years? In environments where a few plant species provide the sole resources for flower-dependent insects in some seasons, failure to flower in unfavourable years could have far-reaching consequences. Can periods of particular network fragility be identified? Also, networks are not static, they are dynamic, with their composition and structure changing over time. How variable is network structure among years? The forb flora of the northern Sahel is dominated by annual species with long-lived seed banks. In such plant communities, seeds of different species may respond differently to germination cues such as the amount and timing of precipitation, so that composition of the forb flora varies among years (Huang *et al.*, 2016). Does such variation affect assemblages of floral visitors? Does the ecological functioning of networks continue despite changes in species composition? In environments like the northern Sahel characterised by strong inter-annual variation, long-term studies are particularly necessary for understanding network structure and dynamics and their effects on ecosystem resilience.

Flowering phenology shapes plants' roles in the resilience of insect–flower networks, and climate change will affect phenology. Long-term phenological studies, supported by weather stations providing basic data on temperature,

humidity, precipitation, and wind, are thus of crucial importance. Altered floral phenology can have cascading effects on many interactions, from those with co-flowering plant species (facilitation or competition) to those with animals (including humans) that are dependent on flowers, fruits, and seeds (Buisson *et al.*, 2017). How common is the intraspecific genetic variation in phenological traits found by Diatta *et al.* (2022) for *Senegalia senegal*? Such variation, along with plasticity, could be a source of resilience to climate change.

Finally, nothing is known about how climate change may impact the phenology of flower-visiting insects in the Sahel and their biotic interactions. What are the life cycles of flower-visiting insects? What are the relative roles of adult resources, including floral rewards, and resources for immature stages in determining insect phenologies? What strategies – for example diapause (Hahn & Denlinger, 2011), restriction to humid refugia (Janzen, 1973), migration (Florio *et al.*, 2020) – allow different species to persist during the dry season? What is known about inter-annual variation in populations of flower-visiting insects in the northern Sahel?

Among the most frequently noted likely effects of climate change on species interactions is phenological mismatch, for example between plants and pollinators (Gérard *et al.*, 2020). Climate change can also lead to phenological mismatch between insects whose adults visit flowers and these insects' larval resources. Studies conducted elsewhere suggest that increased climatic variability makes it difficult for parasitoids to track their prey, resulting in decreased rates of parasitism (Stireman *et al.*, 2005), which would lead to decreased numbers of parasitoid adults visiting flowers. Thus, monitoring the abundance of parasitoids at flowers could provide information about effects of climate change on ecosystem health.

The Sahel has been described as a climate change hotspot (Niang *et al.*, 2014a). Senegal, for example, has already experienced record climatic variability in recent decades (Sultan *et al.*, 2020) and this variability is projected to increase further (Niang *et al.*, 2014a). Arid zones are projected to become more arid, with droughts becoming 2–4 times more frequent depending on the magnitude of warming (IPCC Working group II, 2022). There is thus great potential for effects of climate change on species interactions. In addition to phenological mismatch, climate change could affect plant–pollinator interactions in the region in other ways, *via* the numerous negative physiological effects of high temperatures and increasing aridity on pollinators and plants (Scaven & Rafferty, 2013; Kuppler & Kotowska, 2021).

(2) Do livestock impact insect–flower interactions in the northern Sahel?

Extensive pastoralism is the predominant land use in the northern Sahel, and is frequently implicated as a causal factor of environmental degradation and biodiversity loss. Gebremedhn *et al.* (2023) showed that increasing grazing intensity in northern Senegal led to decreased biomass and diversity of herbaceous plants, reduced vegetation cover, and changes in

community composition. Such changes can affect insects in various ways. Effects of livestock grazing on animals may be direct (e.g. trampling, unintentional predation) or indirect, mediated by effects on plants (van Klink *et al.*, 2015). Several recent studies have reviewed the impact of livestock grazing on biodiversity and on biotic interactions such as those between plants and flower-visiting insects. A recent global meta-analysis showed that grazing reduces plant sexual reproduction, while increasing plant asexual reproduction (Wentao *et al.*, 2023). Another meta-analysis (Filazzola *et al.*, 2020) showed that herbivore exclusion results in increased diversity and abundance of animals, especially of those that are directly dependent on plants such as herbivores and pollinators.

We know of no data describing the impact of livestock on plant–pollinator interactions in the northern Sahel, and we consider this a major gap in research supporting ecosystem restoration efforts in the region. Discourse around degradation in the Sahel has often been framed in terms of the capacity of the soil and the vegetation to support primary production. Less attention has been given to the impact of land use on biodiversity. The study by Gebremedhn *et al.* (2023) is a recent exception. Biodiversity of dryland savannas frequently attracts less scientific attention than that of other environments because of the perception of drylands as bare regions containing low diversity (Durant *et al.*, 2012; Murphy, Andersen & Parr, 2016). Also neglected are the biotic interactions that support multiple ecosystem functions, including pollination and other functions performed by flower-visiting insects. We identify below four outstanding questions about the impact of livestock on insect–flower interactions in the northern Sahel.

(a) *How do livestock-induced changes in vegetation affect the abundance, diversity, and composition of flower-visiting insects?*

Livestock trample soil and create bare ground. While this can negatively impact some arthropod species, it may favour others. For example, bare-soil areas create favourable nest sites for halictid bees. These are among the most important pollinators in the region (Pesenko & Pauly, 2005), and are relatively little affected by habitat degradation (Williams, 2011). Livestock may also alter the abundance, diversity, and composition of floral resources. Some authors have tended to downplay the contribution of intensive grazing and browsing to ecosystem degradation in the northern Sahel, contending that degradation is primarily driven by periodic multi-year droughts rather than overgrazing (Delay *et al.*, 2022; Turner *et al.*, 2023), and that this degradation is reversible, with “regreening” of the Sahel during more humid periods (Brandt *et al.*, 2017). Studies in the Ferlo have shown, however, that grazing and browsing, as well as climate, affect the species composition of herbaceous (Miehe *et al.*, 2010; Gebremedhn *et al.*, 2023) and woody vegetation (Vincke, Diédhiou & Grouzis, 2010) in ways that reflect rangeland degradation. Furthermore, although regreening does occur in wetter periods, species composition is altered and biodiversity loss continues (Dendoncker *et al.*, 2020). Do these changes alter the

abundance and composition of floral resources for insects? Miehe *et al.* (2010) found that heavy grazing favoured the dominance of grasses (wind-pollinated) over forbs (insect-pollinated). By contrast, Gebremedhn *et al.* (2023) found that heavy grazing favoured dominance of forbs, but in particular the dominance of a single invasive forb species, thus increasing the abundance but decreasing the diversity of floral resources. Vincke *et al.* (2010) showed that heavy browsing exacerbated drought effects on trees, reducing their density, size, and diversity, and altering species composition. How these changes affect insect–flower interactions has not been investigated, although studies in East African savannas suggest the impact may be important. In Tanzania, Lasway *et al.* (2022) and Mpondo *et al.* (2023) found that heavy grazing strongly negatively affected the abundance and richness of flower-visiting insects. In Kenya, Guy *et al.* (2021) found that exclusion of wild mammalian herbivores led to large increases in the size and richness of insect–flower networks.

(b) *What are the impacts on insect–flower interactions of changes in the functional composition of livestock assemblages?*

Throughout the drylands of sub-Saharan Africa, populations of browsers (goats and camels) are increasing, while those of grazers (cattle) are decreasing (Rahimi *et al.*, 2022). In Senegal, populations of small ruminants are increasing more rapidly than those of cattle and populations of goats are increasing more rapidly than those of sheep (Zwarts, Bijlsma & van der Kamp, 2023a). Many reasons, including economic, social, and cultural reasons, contribute to these changes. However, the underlying causes may be ecological. Browsers are preferred owing to their ability to tolerate drought and feed scarcity, and to produce meat and milk in all seasons. Goats can forage further from watering points than sheep and cattle (Akinmoladun *et al.*, 2019), and as they are browsers, their food is available throughout the year. They are thus better suited to situations where environmental constraints cause herders to adopt a less-mobile lifestyle. The shift to increasing reliance on browsers is seen as a way to sustain meat and milk production and reduce greenhouse gas emissions in African drylands (Rahimi *et al.*, 2022). However, while greater reliance on browsers may bring immediate advantages, it may also result in greater pressure on forbs (relative to grasses) but especially greater pressure on trees, particularly in the dry season, when lopped-off branches represent an essential source of forage. This increased pressure will have negative impacts on trees (Dendoncker *et al.*, 2024), on the diversity and abundance of floral resources they provide for flower-visiting insects, and on the multiple functions they provide in addition to provision of forage.

(c) *How can the timing of grazing be managed to minimise impacts on plant sexual reproduction and on animals dependent on flowers and seeds?*

The impact of grazing varies depending on the phenophase of the plant. Grazing before plants have flowered has strong negative effects on floral resources (and later, on soil seed banks). Impact of grazing on pollinators can be mitigated by temporarily excluding livestock from particular subplots

during the flowering season (e.g. Farruggia *et al.*, 2012). In the Ferlo, this practice would also serve to create a reserve of dry-season forage, thus providing both biodiversity benefits and a provisioning service for humans. In the Koyli Alpha Community Nature Reserve (ca. 643 ha) in the Ferlo, livestock are excluded, but in the dry season, long after plants have flowered and dispersed seeds, herders are allowed to harvest herbaceous biomass (necromass, as almost all grasses and forbs are annuals). Increasing the number of such areas thus could benefit both herders and biodiversity. Measures proposed to manage the timing of grazing are likely to be more socially and economically acceptable than measures proposing reductions in stocking rate (Enri *et al.*, 2017). Management of timing of grazing must be adaptable, sensitive to spatial heterogeneity in plant phenology, to effects of climate change on the phenology of plants and of flower-visiting insects, and to the fact that grazers can themselves alter plant phenology (Tadey, 2020).

(d) *How can piosphere effects be managed?*

Because livestock must drink frequently, in semi-arid regions their activities tend to be concentrated around watering points. This leads to a pattern of increasing grazing intensity with increasing proximity to watering points (and nearby camps), termed the piosphere gradient (Andrew, 1988). In consequence, areas near watering points have decreased plant

biomass, altered species composition, and decreased plant diversity (Thrash & Derry, 1999). With the increasing density of boreholes in the Ferlo, the proportion of all rangeland that is close to a watering point, and thus subjected to intense grazing, increases, leading to increased rangeland degradation. However, this classical piosphere pattern is accompanied by an opposite gradient: organic matter-rich livestock excrement is also more concentrated in proximity to watering points. In some cases, this can lead to an inverse grazing gradient where plant production is greater in proximity to wells and camps (Rasmussen *et al.*, 2018). Could such positive piosphere effects be harnessed to alleviate negative piosphere effects on rangeland quality (Rasmussen *et al.*, 2018), to benefit both herders and biodiversity? Figure 1 provides a summary of factors affecting insect–flower interactions in the northern Sahel.

(3) **Pollinators for crop plants?**

Crop plants are not as important to subsistence in the northern Sahel as in the agrosilvopastoral lands further south. However, with the trend to increasingly sedentary lifestyles, they are increasing in importance. Drip-irrigated home gardens are becoming more common (Duboz *et al.*, 2019). As home gardens and small agricultural fields around settlements become larger and more numerous, pollination of vegetables and fruit trees will represent an increasingly important ecosystem service. Vegetable species show great

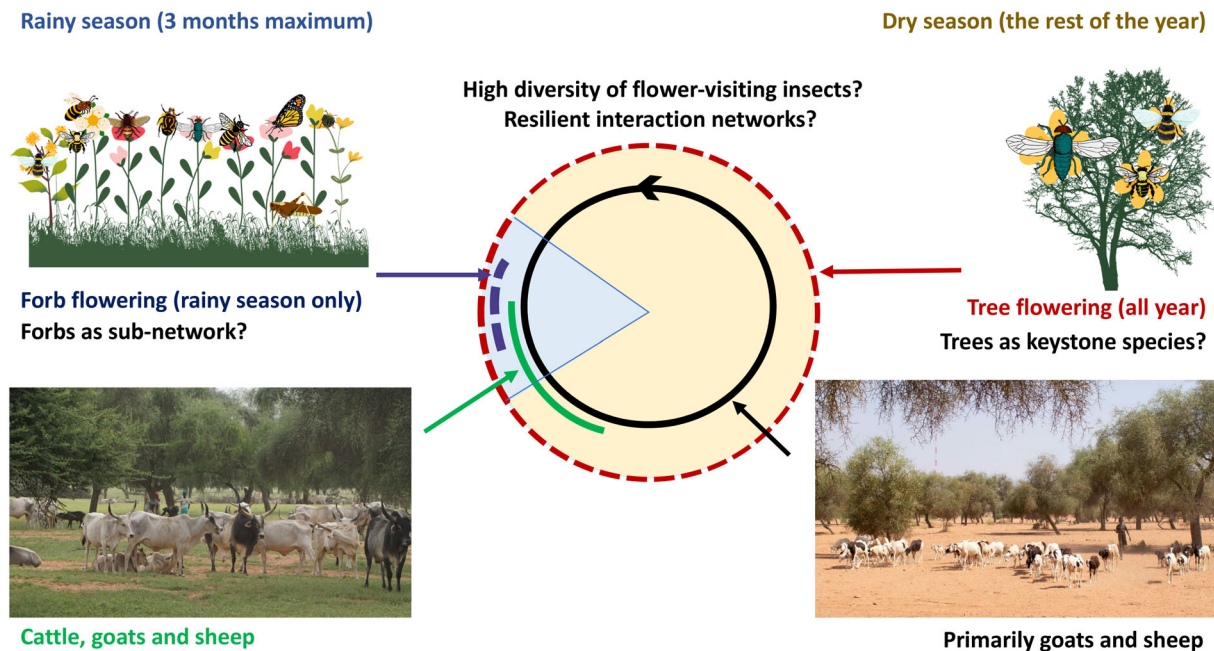


Fig. 1. Factors affecting insect–flower interactions in the northern Sahel. These semi-arid savannas are characterised by extreme seasonality, high inter-annual variation in rainfall and intense grazing by livestock. Herbaceous vegetation is dominated by grasses (wind-pollinated). Flowering of forbs (mostly insect-pollinated) is restricted to the short rainy season, while trees flower year-round and are key for insect persistence. Cattle remain in the area until dry-season forage reserves are depleted. Browsers (particularly goats) predominate in the dry season and are increasingly favoured by herders over grazers due to climate change. The increased pressure they place on trees may weaken networks of biotic interactions such as pollination. Image credits: right, D. McKey; left, N. Medina-Serrano.

variation in their dependence on pollinators; for most fruit trees, and for cucurbits such as watermelon, insect pollinators are essential (Klein *et al.*, 2007; Siopa *et al.*, 2023a,b). In arid northern Tanzania, Sawe *et al.* (2020) found pollination to be limiting for watermelon yields. Whether native insect communities of the northern Sahel can provide adequate pollination services for plants in home gardens is unknown. Also, the increasing adoption of home gardening may be accompanied by more frequent recourse to the use of pesticides, herbicides, and other phytosanitary products. Vigilance will be required in communicating about their benefits and their ecological and health risks (De Bon *et al.*, 2014).

(4) What are the goals of conservation actions?

(a) What is the baseline?

An overarching research priority in the northern Sahel is to determine what conditions conservation actions should attempt to maintain or restore. An ongoing study is revealing a surprising diversity of flower-visiting insects in the Ferlo (N. Medina-Serrano, in preparation). How the current diversity and abundance of flower-visiting insects and the resources they depend on compare to what was present before the changes in climate and land use that began in the 1950s and 1960s will likely never be known. Furthermore, human impacts on plant communities in the Sahel began long before then, with the dawn of pastoralism and then later the wholesale replacement of wild megafauna in the region by livestock. The Sahelian flora is well-known, but some species have become more common and others less common over the last 70 years. In addition, as shown in Table S1, several forb species were introduced and became naturalised in West Africa during precolonial or colonial times (Borokini *et al.*, 2023). Introduced plants can have diverse effects on networks of flowers and insect visitors, from negative (Morales & Traveset, 2009) to positive (Stouffer, Cirtwill & Bascompte, 2014). Their effects on these networks in the Sahel have not been studied.

Reference ecosystems with “near-natural” biodiversity and functioning are lacking in the northern Sahel. Sahelian countries are among the most highly underfunded for biodiversity conservation (Brito *et al.*, 2016). More effectively protected areas could serve as invaluable reference systems for gauging the impact of continued land-use change and climate change on biodiversity and biotic interactions. Rewilding through re-introduction of native wild herbivores could locally restore natural dynamics of these savannas, and modest initiatives have been undertaken in a few small reserves (e.g. Abáigar *et al.*, 2016). In most areas of the northern Sahel, however, the prime objective of restoration will be to maintain biodiversity and ecosystem functioning as effectively as possible in ecosystems dominated by interactions between plants and livestock. In view of the transformation of Sahelian ecosystems by humans and their livestock, defining the “baseline” conditions that actions should aim to

maintain or restore will require a balance between conservation value and realism.

“Baseline” conditions include an inventory of the region’s biodiversity. Species interact, and an accurate inventory of species is essential for understanding interactions. The first step for this region with poorly described fauna is to establish a complete reference base through studies of morphological taxonomy, integrating genetic markers where necessary and possible. Numerous insect species in the region are likely undescribed, and those that have been described may hide cryptic species with different biology. Barcoding of selected insect taxa might greatly add to our knowledge of insect diversity in the region.

(b) Choice of indicator taxa: new strategies for monitoring insect–flower interactions?

What indicator taxa are most suitable for monitoring the effects of climate change, land-use change and conservation actions? For plants, trees appear to be key floral resources ensuring resilience of pollinator networks, but which species may be the most informative indicators of ecosystem health remains unclear. Pertinent insect indicator taxa might include solitary bees, which depend wholly on floral resources for their food. Aculeate wasps and hymenopteran parasitoids, two groups that feed at high trophic levels, should also be good indicators of ecosystem health. However, these groups, particularly the latter, are difficult to identify. Butterflies, less diverse and easier to identify, have been widely adopted as indicator species, but this also has drawbacks (Segre *et al.*, 2023). Food is not the only resource upon which flower-visiting insects depend, with some species having specialised nest-site requirements. For example, some *Xylocopa* spp. nest only in dead stems of a few plant species (Eardley *et al.*, 2009), and grazing and trampling can destroy potential nest sites.

While choosing indicator taxa is a thorny problem, this difficulty is negligible compared to the next step: developing programs to monitor biodiversity by visual identification of these indicator taxa. Even programs that rely on citizen science and unpaid volunteers are costly in time and money, requiring financial and institutional resources that are unlikely to be available in the northern Sahel. One avenue worth considering in regions like the Sahel might be metabarcoding of environmental DNA, using flowers as a substrate. Environmental DNA on flowers can reveal the diversity of insects that visited them, and even the other plants previously visited by these insects (Newton *et al.*, 2023). Monitoring in this way would also not rely on one or a few taxa that may not reflect general patterns. However, this method has not been extensively tested, and its usefulness will depend on the existence of a reference base of the region’s biodiversity of flower-visiting insects.

(c) Promoting diverse communities and genetically diverse populations

How can we promote diverse communities of pollinators and flower visitors, and genetically diverse plant

populations, at the landscape scale? Actions focused on restoring plant diversity also result in restoration of pollinator diversity (Kaiser-Bunbury *et al.*, 2017; Sexton & Emory, 2020), but the effectiveness of this “plant-first” approach in grassland restoration varies among pollinator taxa and restoration methods. Restoration ecologists need to devote more attention to all the ecological needs of pollinators, not only floral resources, and to shaping landscapes that allow pollinators to move between habitat patches, ensuring pollen transfer and gene flow between local populations (Menz *et al.*, 2011). Connectedness between habitat patches may be particularly crucial in arid environments characterised by episodic and spatially highly variable flowering. Encouraging habitat heterogeneity, for example through diverse grazing regimes, will be a key component of any conservation strategy, not only for plants and flower-visiting insects, but for all components of biodiversity. A clear priority in the Ferlo is the conservation of vegetation in the scattered natural depressions that characterise the area. These humid patches harbour greater biodiversity, for example that of trees (Dendoncker *et al.*, 2023), than other habitats in the Ferlo, and constitute refugia for numerous plant and animal species in the face of climate change (Dendoncker *et al.*, 2020).

VI. CONCLUSIONS

- (1) Conducting long-term studies of biotic interactions will be crucial for understanding the dynamics of northern Sahelian ecosystems, which are highly impacted by global changes. Selecting suitable indicators for monitoring interactions and ecosystem health can help assess the impacts of climate change and land-use changes on biodiversity. Trees play a key role in the resilience of insect–flower interactions in this region, due to their year-round flowering and diverse insect visitors. Accurate identification of insect species through morphological and genetic studies will be essential for understanding insect diversity and the ecological roles of component species.
- (2) Under high seasonal and inter-annual climatic variability, understanding flowering phenology and its effects on assemblages of flower-visiting insects is important for identifying periods of fragility in the ecosystem. Climate change can lead to phenological mismatch between plants and pollinators, disrupting pollination networks.
- (3) Nocturnal flower-visiting insects in the Sahel remain completely understudied, but could provide important insights into overall pollination dynamics and thermal adaptations of insects.
- (4) Studies are needed to assess the impact of livestock grazing and browsing on insect–flower interactions in the northern Sahel. Ongoing shifts in livestock composition, particularly the increase in prevalence of goats (browsers), might exert increasing pressure on trees.

- (5) The increasing use of home gardens in the region highlights the need for sustainable practices that ensure adequate pollination services and minimise pesticide use.

- (6) Determining baseline conditions for conservation efforts is challenging but necessary for setting realistic goals that balance biodiversity conservation with human land use.

VII. ACKNOWLEDGEMENTS

This work was supported by LabEx DRIIHM (InterDisciplinary Research Facility on Human–Environment Interactions), which is funded by the French government programme “Investissements d’Avenir” through the ANR, the French national research agency (ANR-II-LABX-0010). We thank the authorities of DRIIHM and of the Observatoire Hommes-Milieus International (OHMi) Tèssékéré, a member of the DRIIHM network. We also thank the IRL 3189 (International Research Laboratory of the CNRS, “Environnement, Santé, Sociétés”), the Institut Fondamental d’Afrique Noire (IFAN), the Département de Biologie Végétale of the Université Cheikh Anta Diop (UCAD) and their staff for their welcome and for organising fieldwork. N.M.-S. was supported by a doctoral dissertation grant from a project funded by Fondation TotalEnergies and administered by the OHMi Tèssékéré, and by additional funding from CNRS Ecology & Environment. The Service de Coopération et d’Action Culturelle (SCAC) of the French Embassy in Senegal funded study visits by A.D. to the CEFE. We thank the local populations of the Ferlo, on whose land we conducted fieldwork, and the Senegalese agency responsible for land management in the region, the ASERGMV (Agence Sénégalaise de la Reforestation et de la Grande Muraille Verte). N.M.-S. thanks her dissertation supervisor, Dr Anne-Geneviève Bagnères-Urbany, for advice and encouragement during this study.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Forb (herbaceous dicot) species in the northern Sahel (Ferlo region, Senegal).

Table S2. Tree and shrub species found in the northern Sahel (Ferlo region, Senegal) inventoried by Niang *et al.* (2014b) and Dendoncker *et al.* (2020).

(Received 29 May 2024; revised 11 November 2024; accepted 15 November 2024)