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Non-Bee Insects as Visitors and Pollinators of Crops: Biology, Ecology, and Management

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Abstract

Insects other than bees (i.e., non-bees) have been acknowledged as important crop pollinators, but our understanding of which crop plants they visit and how effective they are as crop pollinators is limited. To compare visitation and efficiency of crop-pollinating bees and non-bees at a global scale, we review the literature published from 1950 to 2018 concerning the visitors and pollinators of 105 global food crops that are known to benefit from animal pollinators. Of the 105 animal-pollinated crops, a significant proportion are visited by both bee and non-bee taxa ($n = 82$; 77%), with a total gross domestic product (GDP) value of US$780.8 billion. For crops with a narrower range of visitors, those that favor non-bees ($n = 8$) have a value of US$1.2 billion, compared to those that favor bees ($n = 15$), with a value of US$19.0 billion. Limited pollinator efficiency data were available for one or more taxa in only half of the crops ($n = 61$; 58%). Among the non-bees, some families were recorded visiting a wide range of crops (>12), including six families of flies (Syrphidae, Calliphoridae, Muscidae, Sarcophagidae,

Tachinidae, and Bombyliidae), two beetle families (Coccinelidae and Nitidulidae), ants (Formicidae), wasps (Vespidae), and four families of moths and butterflies (Hesperiidae, Lycaenidae, Nymphalidae, and Pieridae). Among the non-bees, taxa within the dipteran families Syrphidae and Calliphoridae were the most common visitors to the most crops, but this may be an artifact of the limited data available. The diversity of species and life histories in these groups of lesser-known pollinators indicates that diet, larval requirements, and other reproductive needs will require alternative habitat management practices to bees.

INTRODUCTION

Most of the crops grown around the world benefit from insect pollination either for the direct production of commodities (i.e., fruit or seed consumed by humans) or in the production of seed required to cultivate the vegetative parts of the crop for consumption (i.e., vegetable seed). The 105 most widely planted crops globally that benefit from insect pollination have greater than US$800 billion gross economic value and include many of the most popular fruit, vegetable, and nut commodities consumed worldwide, such as melons, avocados, berries, and almonds (63; **http://www.fao.org/faostat/en/#home**).

Both wild and managed pollinators provide significant crop pollination services and often complement each other in commercial production systems (8, 32). Bees are the most commonly studied crop pollinators and are thought to dominate many crop pollinator assemblages, in terms of both abundance and diversity (32, 61, 111). Several bee species have been introduced to provide crop pollination services, some of which are managed. These managed species include the honey bees (Apini); stingless bees (Meliponini); *Bombus* spp.; and a few solitary bees, including Alfalfa leaf cutter bees (*Megachile rotundata*), Osmia bees (*Osmia* spp.), and Alkali bees (*Nomia melanderi*). The wild, unmanaged bees that provide crop pollination services include over 700 different species, both social and solitary (32, 61).

There are numerous wild pollinators that are not bees. Myriad non-bees constitute the diverse communities of invertebrate and vertebrate taxa that visit wild plants (78) and cultivated crops (84). Like bees, several non-bee taxa have also been introduced outside of their native host ranges to facilitate the commercial production of specialist crops, such as the *Elaeidobius kamerunicus* weevil for oil palm and fig wasps for fig fruits (11, 107). In addition, some fly taxa are now being specifically reared commercially and managed for the purpose of crop pollination (**http://www.polyfly.es**) and rearing protocols are available for some species, such as Syrphid flies (77). While wild non-bee taxa were recorded in a 2007 synthesis (63), this study did not explore the diversity of non-bee taxa that pollinate globally important food crops, and many studies have since added to our understanding of these lesser-known pollinators.

Different pollinators vary significantly in their pollination performance across crops (32, 84). Understanding which taxa are most effective at transferring pollen is important, as these are the most likely contributors to pollinator-dependent crop yields. While most of these crops have open, easily accessible flowers that are visited by generalist pollinator taxa, some major crop groups have specialized flower morphologies that are likely to limit the effectiveness of some pollinators. For example, poricidal anthers (e.g., many Solanaceae, including tomato and eggplant) require vibration to release pollen, and flower-tripping mechanisms (e.g., papilionoid legumes) are thought to be best pollinated by bee visitors (15). Other crops are pollinated by non-bee insects including, some for which the major pollinator has complex breeding site requirements, such as oil palm (*Elaeis quineensis*), figs (*Ficus carica*), and jackfruit (*Artocarpus heterophylla*) (31, 103),

or habitat requirements, such as fruit husks or decomposing leaf litter to optimize pollination in cocoa (*Theobroma cacao*) (25). Others, such as durian, have flowers that dehisce at night, when bees are generally not in flight (68).

At present, it is challenging to draw general patterns regarding crop pollinator assemblages and their efficiency for all but a small number of crops because efficiency data are lacking. With increasing human population growth and global food demands, understanding the factors that influence the yields of the world's food crops is critical to sustaining ongoing production. In this article, we review the literature to compare and contrast the contribution by bees and non-bees to global food crops. We evaluate the identity and richness of floral visitors, their effectiveness as crop pollinators, and the opportunities and challenges that will likely influence their management in agricultural environments.

We ask the following questions:

1. How diverse are the assemblages of non-bee flower visitors that visit the 105 major animal pollinated crops, and how does this compare to bees?
2. What data are available on the importance of non-bee insects as pollinators?
3. What is the economic value of bee- and non-bee-visited crops to the global economy?

LITERATURE SEARCH AND ANALYSES

Methods

We conducted a literature search based on the supplementary information in the work of Klein et al. (63), selecting the 105 world crops (**Supplemental Table 1**) that benefit from animal pollination for direct production of commodities (i.e., fruit or seed consumed by humans) or that indirectly benefit through the increased production of seed required to cultivate the vegetative parts of the crop for consumption (i.e., vegetable seed). Crops for which the consumed parts are primarily vegetatively propagated were excluded (e.g., potatoes). To minimize duplicate handling of search results for congeneric crops, we grouped crop queries by genera. We grouped together common names and included generic synonyms published in Reference 63 to achieve an exhaustive search and removed ubiquitous words from the search string to improve search precision. The target crops (**Supplemental Table 1**), crop search terms, and associated search notes are listed in **Supplemental Table 2**. For each crop group, we searched the Scopus database from 1950– November 1, 2018 using the query (TITLE-ABS-KEY(pollinat* AND ('crop common names' OR 'crop genus'))). In total, our search queries retrieved 12,680 results. The qualitative results of our flower-visitor family census were unaffected by duplicated references and linked articles. We retained Klein et al.'s list of taxa in our study, which includes additional crop-visitor taxa references not revealed in our search.

Search results were filtered at three levels: (*a*) title and journal, (*b*) abstract, and (*c*) full text. Search results containing unfamiliar specific epithets for crop genera were checked against The Plant List (**http://www.theplantlist.org**) to determine if names were synonyms of target crops. We included visitors to cultivated and naturalized crops as well as crops grown as sentinel or phytometer plants. Non-English titles, abstracts, methods, and results were translated using Google Translate (**https://translate.google.com.au**). Articles were excluded if the titles indicated that the material was not relevant; the majority of these articles focused on nontarget congeneric plant taxa or taxa with shared common names, or were molecular studies published in molecular biology and related discipline journals. For the remainder of the search results, abstracts were scanned for relevance to pollination of the targeted crops. Articles that were clearly focused on animal pollination or were ambiguous in regard to animal pollination were viewed as full text.

Supplemental Material >

We examined the methods to determine if flower visitors were observed directly, or if indiscriminate methods such as pan-trapping or extensive sweep-netting were used to populate crop-visitor lists, in which case such studies were excluded. If articles explicitly stated that particular flower-visiting taxa did not contact the reproductive structures of the flowers, then we did not include these taxa. Some studies did not clearly define their usage of phrases such as flower visitors, but we included these taxa nonetheless. In total, we used data from 1,022 publications in this study.

We used the Global Biodiversity Information Facility (GBIF) species match application program interface (API) (**https://www.gbif.org**) to retrieve taxonomic information for flower-visiting taxa on February 20, 2019. We manually evaluated all returned nonexact, fuzzy logic–based matches against the taxon name recorded from the search. For names not in the GBIF, we checked the source article for taxonomic information, which, if unpublished, was obtained manually through GBIF genera search queries or Google Scholar.

Crop production values were obtained from the Food and Agriculture Organization of the United Nations (FAO) agricultural database (**http://www.fao.org/faostat/en/#home**) for the year 2016 (**Supplementary Table 7**). As the FAO lists multiple commodities derived from single crops, we selected only the single most relevant commodity to represent each of our crop groups. As the contributions of individual crops were unknown from some crop groupings listed in the FAOSTAT database, many crops were grouped as not elsewhere classified (NES) and were excluded in calculations of gross domestic product (GDP) economic value; therefore, estimates of value should be treated as conservative.

Results

Crop flower visitor diversity. At least 20 different animal orders visited the flowers of the 105 listed crops (**Figure 1**; **Supplemental Table 3**). Although insects were the most commonly observed, visitors included vertebrates, such as birds and bats, and non-insect arthropods, such as spiders. Of the 105 crops that benefit from animal pollination, most of the crops are visited by both bee and non-bee taxa ($n = 82$; 77%). Hymenopterans, most of which were bees (**Figure 1**), visited the widest range of crops overall (93%).
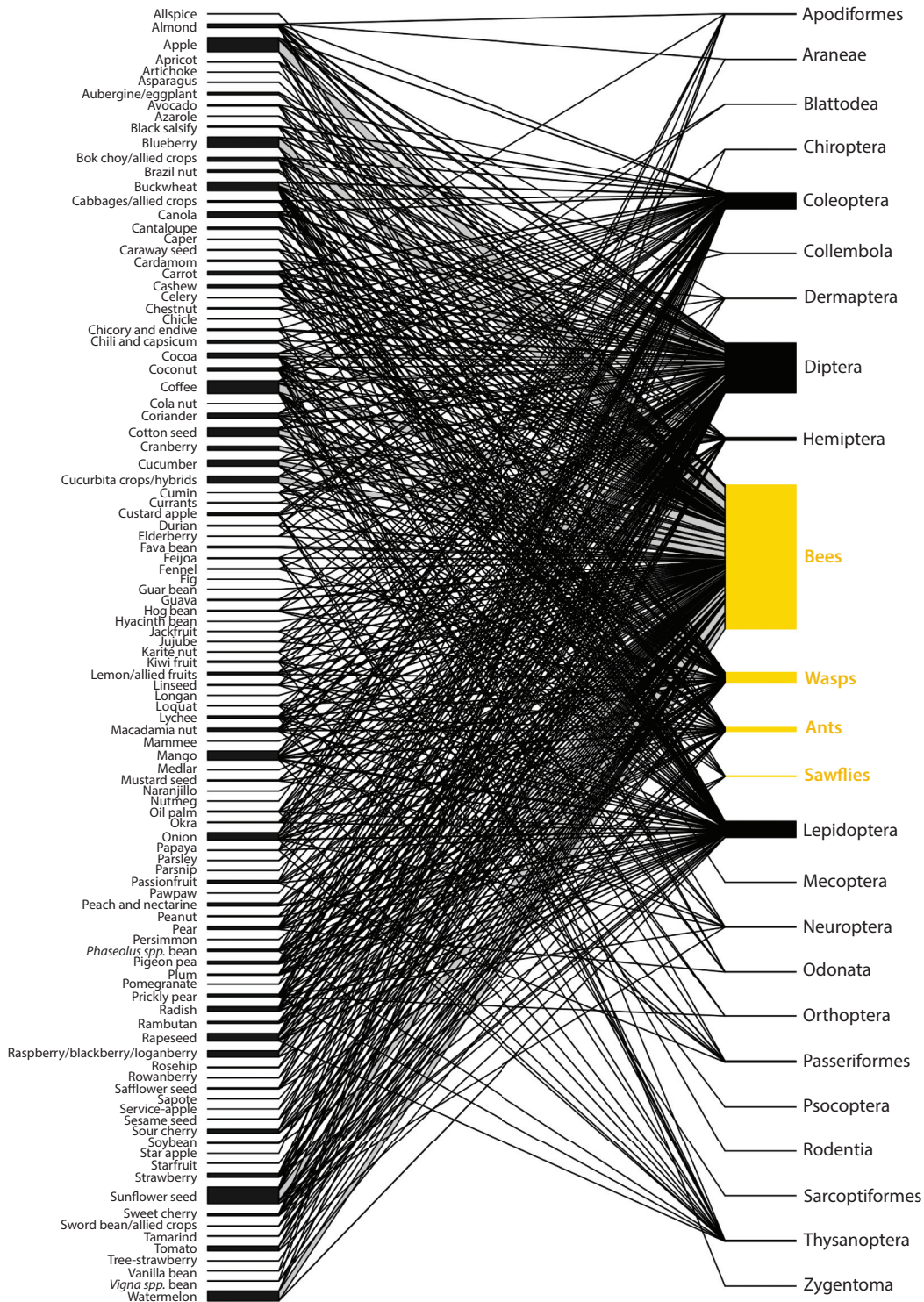
Among the non-bee hymenopterans, Formicidae (ants) were found to visit a large proportion of crops (30%).

Diptera was the second most frequent flower-visiting order (72% of crops), followed by Lepidoptera (54%) and Coleoptera (51%). The fly family Syrphidae (hoverflies) was the most frequent non-bee family, visiting over half of the crop species, followed by the blow flies, in the family Calliphoridae (**Figure 2**).

Coffee was visited by the highest number of insect orders ($n = 10$), followed by buckwheat, bok choy, and allied crops (e.g., Chinese cabbage) and coconut ($n = 9$). Onion and coriander were visited by eight animal orders. Mango, sunflower, cocoa, and coffee had the greatest diversity of families, ranging between 45 and 59 different animal families visiting each of these crops (**Supplemental Tables 3–5**).

While most crops were visited by both taxa, our review identified a small number of major crop species that were visited solely by bees ($n = 15$) or by non-bees ($n = 8$). The crops visited by both bees and non-bees have a total GDP value of US$780.8 billion. The crops visited solely by bees are valued at US$19.0 billion, and those visited solely by non-bees at US$1.2 billion (**http://www.fao.org/faostat/en/#home**; **Supplemental Tables 6** and **7**).

Pollinator effectiveness. Compared to visitation studies, we found relatively few studies that tested differences in pollinator effectiveness among flower visitors (**Table 1**). Efficiency was

Left column (crops):

Allspice, Almond, Apple, Apricot, Artichoke, Asparagus, Aubergine/eggplant, Avocado, Azarole, Black salsify, Blueberry, Bok choy/allied crops, Brazil nut, Buckwheat, Cabbages/allied crops, Canola, Cantaloupe, Caper, Caraway seed, Cardamom, Carrot, Cashew, Celery, Chestnut, Chicle, Chicory and endive, Chili and capsicum, Cocoa, Coconut, Coffee, Cola nut, Coriander, Cotton seed, Cranberry, Cucumber, Cucurbita crops/hybrids, Cumin, Currants, Custard apple, Durian, Elderberry, Fava bean, Feijoa, Fennel, Fig, Guar bean, Guava, Hog bean, Hyacinth bean, Jackfruit, Jujube, Karité nut, Kiwi fruit, Lemon/allied fruits, Linseed, Longan, Loquat, Lychee, Macadamia nut, Mammee, Mango, Medlar, Mustard seed, Naranjillo, Nutmeg, Oil palm, Okra, Onion, Papaya, Parsley, Parsnip, Passionfruit, Pawpaw, Peach and nectarine, Peanut, Pear, Persimmon, *Phaseolus spp.* bean, Pigeon pea, Plum, Pomegranate, Prickly pear, Radish, Rambutan, Rapeseed, Raspberry/blackberry/loganberry, Rosehip, Rowanberry, Safflower seed, Sapote, Service-apple, Sesame seed, Sour cherry, Soybean, Star apple, Starfruit, Strawberry, Sunflower seed, Sweet cherry, Sword bean/allied crops, Tamarind, Tomato, Tree-strawberry, Vanilla bean, *Vigna spp.* bean, Watermelon

Right column (taxa):

Apodiformes, Araneae, Blattodea, Chiroptera, Coleoptera, Collembola, Dermaptera, Diptera, Hemiptera, **Bees**, **Wasps**, **Ants**, **Sawflies**, Lepidoptera, Mecoptera, Neuroptera, Odonata, Orthoptera, Passeriformes, Psocoptera, Rodentia, Sarcoptiformes, Thysanoptera, Zygentoma

(Caption appears on following page)

A crop–flower visitor network. The width of the bars is based on the number of taxa found to visit that crop group in the literature reviewed; the wider is the bar, the more taxa visited that crop. The yellow bars and labels represent the groups that make up Hymenoptera.
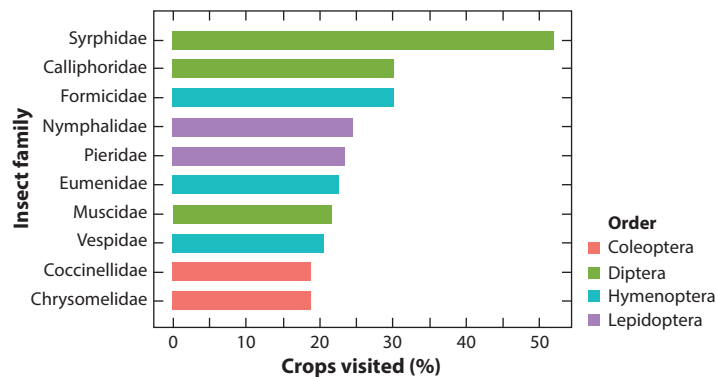

Figure 2

Top 10 non-bee flower visitors by percentage of major crops visited.

measured as pollen deposition on floral stigmas (36 crops for bees, 19 for non-bees), fruit set after caged pollinator or exclosure trials (39 crops for bees, 15 for non-bees), estimates of pollen carried in bee corbiculae or nests (23 crops for bees only), or pollen carried on visitor bodies (not including scopa or corbiculae) (36 crops for bees, 24 crops for non-bees). At least one of the metrics for measuring non-bee effectiveness was only measured in 30 crops. The two effectiveness metrics that included direct estimates of pollen delivered to plants (i.e., fruit set and pollen deposition of stigmas), as opposed to indirect measures of pollen transfer (i.e., body pollen, pollen carried in scopa/corbiculae), were estimated in only 15 crops for non-bees.

Discussion

Our review of the literature indicates that among the many and diverse non-bee pollinators, flies (especially from the families Syrphidae and Calliphoridae; see **Table 2**) are the most common and visit the widest range of crops. As flies and bees belong to entirely different orders, there are

Table 1   Number of crops for which data are available on effectiveness of non-bee flower visitors as pollinators

Method of estimating effectiveness or importance	Number of crops for which data are available	
	Bees	**Non-bees**
Single-visit (or multiple-visit) pollen deposition	36	19
Seed or fruit set in cage trials	39	15
Body pollen	36	24
Corbicula and scopa or nest pollen (bees only)	23	NA
Other methods (e.g., correlations of open fruit set with visit rate)	17	9

Abbreviation: NA, not applicable.

Table 2 Life history traits of five fly species that commonly visit a variety of crops

Species	Number of crops visited	Larval life history	Life cycle, generations, and adult longevity	Adult seasonality	Hibernation	Habitat and geographical range	Fecundity	Migratory
Eristalis tenax (Linnaeus, 1758)	28	Inhabit broad range of aquatic and semi-aquatic habitats, e.g., manure, compost, slurry	Typically multiple generations (>2/year) (23) Adult female lifespan is 3 months in the lab without hibernation Egg to adult in 24–36 days (at approximately 21.5°C) (77)	Almost entire year, including mild winter days	As adults	All continents except Antarctica, common in intensive agro-ecosystems (98)	3,000 eggs/female in 2 months (77)	Highly
Episyrphus balteatus (De Geer, 1776)	24	Feed on many aphid species, as well as Caccoidea, Phyllaxeridae, and Psyllidae (36) Found on a wide range of plant species	Typically multiple generations (>2/year) in Europe (23) Egg to adult in 21.2 days (at 26.6°C) (46) Adult female longevity of 38 days or more (greenhouse) (35)	In Europe, ~10 months/year Adults active on milder winter days	As adults	Occurs across a wide range of habitats, including agro-ecosystems (96); present across Europe, North Africa, Asia, and Australia	780 eggs/female in greenhouse (35)	Highly

(Continued)

Table 2 (Continued)

Species	Number of crops visited	Larval life history	Life cycle, generations, and adult longevity	Adult seasonality	Hibernation	Habitat and geographical range	Fecundity	Migratory
Eristalinus aeneus (Scopoli, 1763)	10	Inhabit various aquatic habitats (e.g., ponds, coastal lagoons, rivers, irrigation ditches), including hypersaline environments, dung, and sewage	Typically multiple generations (>2/year) in Europe (23) Female average lifespan is 31.1 days in the lab Egg to emergence is 22.5 days at 20–22°C (76)	Active approximately 5–6 months during warmer months in Europe	As adults	Europe, Africa, Asia, Australia, and North Africa Found in a wide variety of habitats but restricted to coast in northern Europe	Not available	Non (23)
Sphaerophoria scripta (Linnaeus, 1758)	9	Mainly ground layer aphids (90) Found on a wide range of plant species	Typically multiple generations (>2/year in Europe) (23)	5–7 months in Europe	Apparently puparium in grass roots	Wide range of habitats, including agro-ecosystems	Average of 365 eggs/ female in the lab (20–22°C) (76)	Highly
Calliphora vicina (Robineau-Desvoidy, 1830)	8	Feed on various carrion and processed meats (22)	Egg to adult in 15–22 days at 10°C (18) Multiple generations/year, but dependent on weather (1) Adult longevity is 93–128 days (79)	Most abundant in the spring and summer months, but also occurs in winter (49)	Overwinters as larvae, pupae, or adults (1)	Occurs in common urban habitats (52) and woodland (42) and across all continents but Antarctica (19)	Approximately 2,000 eggs/ female (88)	Not available

many differences in their biology, and it is important to recognize that there are therefore different challenges and opportunities in how they can be managed for crop pollination outcomes. There is also a great diversity within each of these clades; thus, while we can make generalizations, each crop and potential pollinator will have its own particularities.

Bees depend entirely on floral resources for both larval and adult stages, while most flies and many other non-bee flower visitors do not. Of the non-bees identified as commonly visiting crops in this review, adults primarily use floral resources (and then mostly nectar), whereas non-bee larval lifestyles are widely variable, even within families. Syrphidae are dominated, but not exclusively so, by species with either predacious larvae (consuming aphids and other small soft-bodied insects) or larvae living in aquatic or semiaquatic environments feeding on a broad range of organic material (**Table 2**). The larvae of many Calliphoridae feed on a range of carrion but also include species parasitic on earthworms (*Pollenia* spp.) (101) and those that feed on the larvae and eggs of other insects (*Stomorrhina* spp.) (112). The larger flies that typically visit the flowers of many crops have larvae that feed on resources that are common in agricultural landscapes—aphids, dung, and decaying organic matter (**Table 2**). Lepidopterans often have specific host–plant relationships for larval feeding, and as a consequence, agricultural intensification at landscape scales often favors species with more general host-plant larval feeding requirements (70). Flower-visiting beetles also have a wide variety of larval food preferences, reflecting the high taxonomic diversity of flower-visiting taxa (58, 67), and several taxa are known to use fruit as food and/or brood sites (57, 103).

Many non-bee insect pollinators, such as flies, butterflies, and beetles, are capable of large flight distances relative to most bees. This is in part because non-bee insects do not provision young and maintain nests, as do bees (the exception being some non-bee hymenopterans). Because bees provision their young with pollen, the larvae remain in the nest or colony, and the adult bees have an attachment that limits their freedom to move. This attachment is strongest for the social bees with perennial colonies, but even for solitary bees, adult females return to the nest repeatedly during establishment (74). Among the bees, only some larger-bodied species are known to travel great distances (e.g., 50 km for Euglossine bees) (82), while most have a foraging range under 1 km (33, 38, 95, 113). In contrast, long-distance flights of between 50 and 110 km have been recorded for Syrphid flies, including *Episyrphus balteatus* and *Sphaerophoria scripta* (2, 34). Such travel distances may be important with regard to the role of non-bee insects in transgene flow (83).

Dipteran pollinators, in particular Calliphoridae and Syrphidae, are also capable of quickly responding to changes in resource availability through high mobility, high fecundity, and short life cycles. Hoverflies, for example, are capable of producing several generations per year (**Table 2**). As a consequence, some flies that visit many crops produce multiple generations per year and produce eggs numbering in the thousands per female (**Table 2**); bees will typically have fewer generations per year and fewer offspring produced (26, 74). As bees need to provision their larvae with pollen, they generally invest in fewer but relatively larger eggs compared with flies. At the extreme, some *Xylocopa* produce eggs that are approximately half the length of the adult female's body (74). These different tendencies in reproductive strategy would generally be expected to permit the flies to have faster population growth rates than bees when conditions are suitable.

While there are indeed species of social bees (particularly *Apis* spp.) that share information on foraging opportunities in the colony and then recruit to those resources in large numbers, this level of social behavior is not common among bees, and in fact, the majority of bee species are solitary (i.e., no social structure) and therefore do not share information (21, 74, 87). Thus, while the social bees have higher reproductive potential than other bees and many flies if compared on an individual-to-individual basis, the performance of the queen needs to be judged relative to the whole colony's labors that support her.

Bees and flies also exhibit marked differences in flower foraging behavior (54). These differences are particularly important in hybrid seed crops, which require movement between rows of intermixed plantings of outcrossing crops. For example, in vegetable hybrid seed crops, both honey bees and wild bees often show preferences for one line over the other (50) and do not frequently move between the lines (66). Non-bees have been found to move between male and females lines in vegetable hybrid seed production systems more regularly than do bees (29).

Many flies have worldwide distributions, including the major crop-visiting fly families and the five fly species that most commonly visit crops (**Table 2**), suggesting that they are well adapted to transformed landscapes. *Eristalis tenax* originated in Europe or the Middle East and now has a global distribution, a history shared with many other imported crop pollinator taxa, such as houseflies (*Musca domestica*) and some blowflies (*Calliphora* spp.). This has facilitated their expansion into many agricultural and urban environments, where they have been recorded as flower visitors and pollinators (41, 98).

Responses of bee and non-bee pollinators to agricultural environments are complex and understudied (92), and generalized patterns that hold across multiple pollinator taxa and crop types are difficult to identify (4, 45). Nonetheless, different insect taxa respond differently to changes in surrounding land use (62, 97). Landscape intensification filters pollinators by functional traits favoring generalist feeding habits and larger body sizes (30). For bees, there is strong evidence to suggest that richness and visitation rates to crops decline with increasing distance from natural habitats (86), likely due to nesting and nutritional habitat needs that are limited in agricultural fields (110). For example, many solitary bee species are ground nesters (74) and can thus be impacted by farm management methods such as frequent tillage (104), while a few more tolerant bee species, such as some *Lasioglossum* spp. (27, 40), remain in highly transformed landscapes. In contrast, hoverfly diversity appears to be less negatively impacted by changes in land use than diversity of other taxa, and many hoverfly species have been found to benefit from crop production (55). Some studies find that hoverfly assemblages maintain species richness and abundance away from remnant and seminatural vegetation, in contrast to wild bees.

In some agricultural systems, specific habitat patches have been shown to be important for non-bee pollinators. Proximity to rainforest influenced the assemblages of pollinating beetles that visited atemoya flowers in tropical Australia (5). Increased hedgerow cover at the landscape level was associated with greater hoverfly visitation rates and enhanced pollination of plants, as well as reduced abundance of crop pests (17). However, hedgerows can also act as a barrier to pollinator movement (60).

KNOWLEDGE GAPS AND RESEARCH PRIORITIES

Nocturnal Pollination

Despite nocturnal pollination occurring in plant species from 30% of angiosperm families (7), the contribution of nocturnal animals to crop pollination has rarely been examined (16, 64). The role of moths may be particularly underestimated. They are considered the most speciose order of flower-visiting insects (approximately 123,000 species versus 17,000 bee species; 108) and are considered pollinators of at least 289 plant species (69). Crops for which nocturnal pollinators have been recognized as important include papaya (moths) (72), *Agave tequilana* (bats) (102) and durian (bats and nocturnal bees) (109). Each of these crops has floral characteristics expressed more strongly at night, e.g., papaya flowers open at dusk and are typically more strongly scented at night than during the day (20); paniculate agaves (e.g., *A. tequilana*) typically produce large quantities of nectar and pollen at night (94); durian anthers dehisce in the evening, pollen viability then steadily decreases (109), and floral structures abscise by morning (47).

Nocturnal pollination may also be more important than is generally recognized even for crops with prominent daytime pollinators. Moths carry pollen that suggests that they are at least flower visitors of various crops, including *Brassica/Raphanus* (69), and nocturnal pollination may support fruit set in lowbush blueberry *Vaccinium angustifolium* (16). Moths are also suggested to be pollinators of *Lonicera caerula* (Haskap) cultivars, as some flowers open in the evening and are still open in the morning (28).

For those crops that allow pollination across the day–night cycle, nocturnal pollinators might prove to be significant as a compliment to the services of diurnal pollinators. However, the paucity of studies assessing nocturnal pollination in crops limits our ability to develop strategies for growers to manage pollinators to optimize nocturnal pollination.

The Importance of Small Non-Bee Insects as Crop Pollinators

Small non-bee insects (defined as having body length smaller than 3 mm) are also key pollinators of a small number of crops, including cocoa (*T. cacao* L.), pollinated by *Forcipomyia* midges (37); fig (*Ficus* spp.), of which some varieties still depend on pollination by fig wasps (subfamily: Agaonidae) (14); and jackfruit (*A. heterophyllus* Lam.), pollinated by the gall midge *Clinodiplosis ultracrepidata* Gagné (Cecidomyidae) (31). The flowers and inflorescences of both figs and jackfruit also support the larval stages of their pollinators. Fig wasps oviposit within the inflorescence (syconium), where the larvae then develop (89), while fungus-infected male flowers of jackfruit provide a brood site and larval nutrition for their midge pollinators (31). Thrips (Thysanoptera) have been implicated in the pollination of 24 crop species (59). In other crops, small non-bee insects were not found to contribute significantly to pollination. For example, while studies have reported high abundances and diversity of small insects (particularly Diptera and Thysanoptera) within flowering crops, including pak choi (*Brassica rapa* ssp. *chinensis*) (51), onion (*Allium cepa*) (106), and carrot (*Daucus carrota*) (6), they were not found to contribute significantly to pollination. For some of the crops where small non-bee pollinators are thought to play an important role, habitat management is important to support high abundances in orchards. For example, management strategies to support *Forcipomyia* midges in cocoa include the provision of moist, decaying organic material within orchards, the provision of shade, and the minimal use of insecticides (narrow rather than broad spectrum) (12). Overall, we have little knowledge of the species of small non-bee insects that visit crops, apart from a few key crop species, and little to no knowledge of their effectiveness in most crops.

Limited Data Availability: Pollinator Efficiency and Gene Flow

Most records of non-bees visiting crops are no more than observations of insects visiting flowers. Few studies provide data relating to pollen deposition or fruit or seed set estimates after visitation by specific taxa (**Table 1**). While we know that quantity and quality of pollen transferred varies among taxa (34, 84), this area deserves significant further research. Both bee and non-bee insects also act as significant flower visitors and pollinators of many wild and cultivated plants that are generally assumed to be wind pollinated or autogamous, such as rice (83). Insect visitors to these crops can affect gene flow even if they have little influence on overall fruit set, so they deserve more attention, particularly in this context.

MANAGEMENT OF NON-BEE POLLINATORS FOR AGRICULTURE

Given the roles for non-bee pollinators indicated by our review, we advocate the use of two broad categories for non-bee pollinator management: (*a*) management for generalist-pollinated crops,

dominated by medium to large flies, and (*b*) management for crops with more specialized associations with flower visitors, such as beetles, thrips, and small fly pollinators.

As floral resources are limited in many agricultural habitats, schemes encouraging wildflower strips have been implemented in many parts of the world to enhance biodiversity and connectivity in agricultural landscapes (3, 24, 48, 65). Identifying suitability of different flower resources is important because studies have shown that, even when many different flowers are available, bees do not collect pollen from all species (39). While it is well established that bee colonies require a balanced diet with high protein for optimal larval development (9, 43), and floral richness has been found to be important to hoverflies at the local scale (93), we know relatively little about floral resource needs of non-bee flower visitors.

Many non-bee flower visitors across several different orders have partially aquatic life histories (85) including *E. tenax*—one of the most important non-bee pollinators globally. *E. tenax* and other members of the Eristalinae subfamily of the Syrphidae begin their life feeding on decaying organic matter in semiaquatic habitats (96). Agricultural habitats that provide resources for the development of these larvae include ponds (99); effluent holding pits; and streams containing sewage, decaying vegetation, or carcasses (80). Syrphid abundance has been specifically associated with pond habitats in agricultural landscapes and strawberry pollination (99). The effective management and conservation of these habitats is thus an important component of management strategies to cater to non-bee pollination services.

Management practices in the broader landscape can also be modified to promote particular taxa. Less intensively managed grasslands are associated with higher syrphid abundance and beetle species richness, perhaps in response to increases in plant height and leaf litter (93). Similarly, management practices such as delayed summer cutting of grasslands to provide extended flower forage resources and providing uncut refuge areas have been found to promote hoverfly abundance and diversity (73), and staggered mowing of road verges to leave these habitats undisturbed when they are especially productive promotes abundance of bee and non-bee pollinators (13). The diversity and abundance of moths have been shown to decline with grassland intensification (increased fertilizer use, grazing, and mowing), although host generalists were less affected; the structure of the moth community depended in part on whether the grassland was animal grazed or mowed (70). As well as diversification of pastures and grasslands, non-bee pollinators are likely to respond positively to mixing and alternating grazing intensity practices at the local and landscape levels. At the landscape scale, however, floral resource effects on syrphids might be moderated by availability of prey for the predaceous species (91). It may also be that the high mobility of some syrphids, such as *E. tenax*, allows populations to exploit widely scattered resources (71).

One of the most promising benefits of integrating non-bees into agricultural cropping systems is the potential for synergies across other ecosystem services, such as biological control of pests (10, 56). One of the major groups of the Syrphidae—the Syrphinae—are both pollinators as adults and predatory at larval stages on aphids and other major crop insect pests (44). In times of few floral resources, honeydew from aphids may also be utilized as an additional energy source by adult hoverflies (105). Other insect taxa that have dual roles as crop pollinators and pest predators include wasps and tachinid flies (53, 62) if flowering phenology is matched with pest egg availability (75). These complementary services have the potential to reduce the cost to growers by reducing the need for pesticide applications, which may reduce pressure on other beneficial insect pollinator groups utilizing the local environment (81).

Finally, careful planning needs to accompany decisions and strategies to promote non-bee pollinators, as some pollinating fly species can spread disease and negatively impact other types of agricultural production, such as livestock (e.g., blowfly strike; 100). Nitidulidae beetles may be

fruit pests, and many flower-visiting butterflies, e.g., cabbage whites, are also crop pests. Identifying the trade-offs and identifying effective management options under these conditions are important first steps.

In conclusion, non-bee taxa are important contributors to many global food crops, yet significant knowledge gaps exist with respect to the identity and efficiency of these taxa. These limitations make it difficult to target the management of specific pollinators for specific crops or to estimate the economic value of these taxa to crop production worldwide.

The diversity of resources required for non-bee as well as bee reproduction means that farm-level as well as landscape management is critical to close the yield gap and create sustainable agricultural systems and communities. Targeting specific pollinators for specific crops will require further research evaluating the efficiency and life history needs of diverse taxa and how these vary in time and with the scale of habitat quality.

DISCLOSURE STATEMENT

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