

ARTICLE

Crop-pollinating Diptera have diverse diets and habitat needs in both larval and adult stages

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Abstract

Insects are important pollinators of global food crops and wild plants. The adult and larval diet and habitat needs are well known for many bee taxa, but poorly understood for other pollinating taxa. Non-bee pollinators often feed on different substrates in their larval and adult life stages, and this diet and habitat diversity has important implications for their conservation and management. We reviewed the global literature on crop pollinating Diptera (the true flies) to identify both larval and adult fly diet and habitat needs. We then assembled the published larval and adult diets and habitat needs of beneficial fly pollinators found globally into a freely accessible database. Of the 405 fly species known to visit global food crops, we found relevant published evidence regarding larval and adult diet and habitat information for 254 species, which inhabited all eight global biogeographic regions. We found the larvae of these species lived in 35 different natural habitats and belong to 10 different feeding guilds. Additionally, differences between adult Diptera sexes also impacted diet needs; females from 14 species across five families fed on protein sources other than pollen to start the reproductive process of oogenesis (egg development) while males of the same species fed exclusively on pollen and nectar. While all adult species fed at least partially on floral nectar and/or pollen, only five species were recorded feeding on pollen and no fly larvae fed on nectar. Of the 242 species of larvae with established diet information, 33% were predators ($n = 79$) and 30% were detritivores ($n = 73$). Detritivores were the most generalist taxa and utilized 17 different habitats and 12 different feeding substrates. Of all fly taxa, only 2% belonged to the same feeding guild in both active life stages. Our results show that many floral management schemes may be insufficient to support pollinating Diptera. Pollinator conservation strategies in agroecosystems should consider other non-floral resources, such as wet organic materials and dung, as habitats for beneficial fly larvae.

KEYWORDS

Diptera, ecosystem processes, non-floral habitat, pollination, pollinator management, resource supplementation

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INTRODUCTION

Bees, flies, and other insects are all important pollinators of global food crops and wild plants, as they are regular flower visitors as adults (Rader et al., 2020). To support resident populations of wild and managed bees, many agri-environment and habitat restoration schemes in farmland thus largely focus efforts on the planting of floral resources (Batáry et al., 2015). Since adult bees provision larvae in nests or hives with floral products (e.g., nectar and pollen), bee larvae are thereby expected to benefit from the same resources that adult bees need (Batáry et al., 2015); however, other insect pollinators, such as flies, wasps, moths, and beetles, generally feed upon different resources in their larval and adult life stages (Truman & Riddiford, 1999). This, coupled with the fact that most non-bee pollinators do not provision their offspring, suggests the larval and adult life stages of other pollinators rarely use the same resources or occupy the same habitats (Truman & Riddiford, 1999). This further means that practices supporting pollination service delivery, such as floral strip agri-environment schemes (Batáry et al., 2015), may only support the adults, but not the larvae of non-bee pollinator taxa.

The differences between developmental stages of pollinating insects have significant implications for management supporting various other non-bee taxa. Diverse diet and habitat use across different life stages mean that non-bee taxa use a greater range of food resources and occupy a greater number of different habitats compared to bees (Klomp, 1964). Specifically, many crop-pollinating Diptera contribute to ecosystem services beyond pollination, both in their adult and larval stages of development (Adler & Courtney, 2019; Cook et al., 2020). For example, larvae of Syrphidae (Mushtaq et al., 2014; Pekas et al., 2020), as well as adults of Empididae (Mclachlan et al., 2003), some Muscidae (Morris & Cloutier, 1987), and Scathophagidae (Buser et al., 2014), are natural enemies of pests within crops. Further, the larvae of Sarcophagidae (Goto & Numata, 2009), Stratiomyiidae (Raksasat et al., 2020), Calliphoridae (Paczkowski et al., 2015), and Muscidae decompose carrion, recycle organic matter, and increase nutrient cycling (Ogbalu, 1999). However, overall, the larval stages of many flies are poorly known on a global scale.

Many flies are efficient crop pollinators that are ubiquitous, occur globally, and contribute to multiple ecosystem services in agroecosystems (Dunn et al., 2020; Van Oystaeyen et al., 2022). Some fly species also complement bee inactivity within cropping systems, as the two taxa generally visit flowers at different times of the day and have different activity patterns based on season (Brittain et al., 2013; Lee & Kang, 2018). Also, unlike most bees,

apart from bumblebees which have thermally insulated hairy bodies (Heinrich, 1972; Lundberg, 1980; Oyen et al., 2016), flies can generally visit flowers at lower temperatures (Kühnel & Blüthgen, 2015; Lee & Kang, 2018; Totland, 1994) higher altitudes (Goodwin et al., 2021; Totland, 1994), and in inclement weather (Brittain et al., 2013; Goodwin et al., 2021). Additionally, flies are generally able to move freely within landscapes as adults (Bell, 1990), which differs from bees who are confined to their hive or nest sites (Klein et al., 2017). These different life history needs for the same species can be advantageous in diverse environments (Yin et al., 2019), but they can also be disadvantageous in environments with low habitat diversity or those that have limited nutritional resources, such as heavily managed agricultural landscapes. For example, when one feeding stage lacks a required resource (e.g., larvae do not have sufficient substrates to feed on or adults do not have a suitable place to lay eggs), the persistence of the local species population may be compromised. Therefore, understanding the resource needs required by all feeding stages of other pollinators is necessary to support pollinator diversity more broadly.

Here, we use Diptera to better understand life history needs of non-bee pollinator taxa and their implications for the habitat requirements and conservation of the world's pollinators. We conducted a global survey of crop-pollinating Diptera to ask the following questions:

1. What are the specific diet and habitat needs of larval crop-pollinating fly taxa?
2. Do larval and adult feeding guilds contribute to the same or different ecosystem processes (i.e., predation, herbivory, pollination)?
3. What is the current availability and quality of global fly life history data to inform future intervention schemes for the management of Diptera?

To answer these questions, we reviewed the literature on adult and larval diet needs, larval habitat needs, and biogeographical region of origin for 242 crop-pollinating adult Diptera species (Davis et al., 2023).

METHODS

Diet and habitat literature search

We recorded 431 crop-pollinating Diptera species from 1477 publications using the a global review study (Rader et al., 2020) and the global, public database CropPol (Allen-Perkins et al., 2022). For this study, we only utilized the records with species-level taxonomic data as

some flies even within the same genus have been shown to have different life histories. Also, as flies are notoriously difficult to identify and the diversity of crop visiting flies is high, family-level taxonomic resolution was most common in the databases we used; thus, while we acknowledge that these findings are likely a gross underestimate of the true diversity of fly species visiting crop flowers, this largely reflects the taxonomic resolution present in the global databases.

All species collected from both databases were recorded visiting the flowers of at least one global crop system as adults. Each of the 431 species were searched by the species' name in both the Catalogue of Life and Global Biodiversity Species Checklist for accepted species names. If no results were found in either database, we searched the species name in Google Scholar. The original list collected from the literature was thus condensed to 405 species (Appendix S1: Table S1).

We then used Scopus and Web of Science to determine first larval and adult diets, and then larval habitat information according to evidence for all 405 species. Each species was first searched in *Scopus* (6 July 2020) using the species' name and data extracted from the resulting papers. For all species in which there were no search results or no relevant papers in *Scopus*, we conducted the same species' name search in all databases of Web of Science (14 January 2021) using the same methodology. Papers were included if they described (1) species-specific larval feeding substrate(s), (2) adult feeding substrates that differed from floral pollen and/or nectar, (3) the habitat(s) the fly larvae have occupied, and (4) crop visitation records not included in (Rader et al., 2020) and the CropPol database (Allen-Perkins et al., 2022).

If there were 50 or more papers to filter for a species, the search terms "diet*," "larva*" and "habitat*" were added to the search and the resulting papers were filtered via the abstracts. If we were unable to confidently identify natural feeding substrates of larvae reared on artificial diets, we considered the feeding substrate the predominate component of the diet. Studies which recorded larviparous taxa (i.e., those that lay first-instar larvae instead of eggs) and female flies being attracted to baits were only included if the authors observed the adults larvipositing. Studies with restricted access to the methodologies and results were not included. Articles that were not written in English were translated using Google Translate, and if relevant information was unclear, then the article was also not included.

We considered the habitat the ecospace (ecological space) of the larval stage of the fly (Brunbjerg et al., 2017). We further categorized the habitats as natural, human-modified, or artificial habitats (Appendix S1: Table S2). For

this meta-analysis, we considered natural habitats any area or substrate that was not created by anthropogenic activities (e.g., wetlands, decaying plant materials, carrion, etc.). Human-modified habitats were defined as any area or substrate altered, either directly or indirectly, by anthropogenic activities (e.g., sedimentation basins, sewage, effluent, etc.). Artificial habitats were defined as those entirely created by people inside the controlled conditions of a scientific laboratory.

In total, our search terms yielded 3039 results on larval diet and habitat information. The relevant papers from these results, combined with the adult crop visitation papers from both reference databases, yielded 1067 papers included in our current database (Appendix S1: Figure S1). Additionally, we were unable to recover larval diet information for 163 of the 405 species and we did not recover habitat information for 151 species using our search criteria. Therefore, in our results we analyzed the larval diet needs of 242 species, and the larval habitat needs of 254 species (Davis et al., 2023).

Determining ecological feeding guilds and processes

We used the specific feeding substrates collected in the literature to best infer the ecological feeding guilds of both feeding stages for each fly (Appendix S1: Table S3). Only the feeding substrates were used to infer feeding guilds, as we found many fly larvae with different feeding guilds live in the similar habitats. We did not infer ecological feeding guilds for flies fed semi-synthetic or synthetic substrates when the exact component that sustained the fly larva was unclear (Appendix S1: Table S4); therefore, we excluded the larvae with unknown feeding guilds from our analysis.

We further used the feeding guilds to determine the potential processes (e.g., pollination, herbivory, predation) supported by the fly species (Saunders et al., 2016). Coprophages, detritivores, and necrophages were placed in the decomposition group as animals with these feeding habitats break down organic materials and recycle nutrients. Fungivores were placed in an indeterminate group as we were unable to determine what function flies with this feeding habit had in an ecosystem. Hematophages were placed under the pathogen group, as animals with these feeding habitats can be disease vectors (Blitzer et al., 2012). Similarly, we placed parasites and parasitoids under the pathogen group, as Brian et al. (2022) demonstrated that parasites can alter wider ecosystem processes by changing the phenotype of their host and should thus be integrated into ecosystem process analyses.

Determining biogeographical regions

This is a global review and includes species likely restricted to specific biogeographic regions, while other species are more widespread in geographic range distributions. We therefore searched for the biogeographical regions each species is known to inhabit. For species known to inhabit the Australasian, Antarctic, Oceanian, and Nearctic biogeographic regions, we searched online catalogues and monographs (Appendix S1: Table S5). For all other biogeographic regions without available species catalogues (Afrotropical, Neotropical, Palearctic and Indomalaya), we searched the biosystematics database *Systema Dipterorum* (<http://www.diptera.org>), managed by experts in the field of fly taxonomy and systematics. With this search criteria, we recovered biogeographical data for 235 of the 242 species included in our global database.

Reliability of larval diet information

For all relevant sources, the quality of the evidence in each reference was rated for the diet information only. Each paper was then classified in one of four categories: “inferred,” “validated,” “inaccessible,” or “expert.” Inferred evidence was used to describe statements made by authors within the study about the diet, but these statements were not clearly supported by data in the paper. Validated evidence meant the fly was physically observed feeding on the specific diet or reared on the substrate in the controlled conditions of a laboratory. Inaccessible evidence meant we could not access the paper, or the fly was reared in a laboratory under an “artificial diet,” but the specific contents of the diet were not listed. Finally, expert evidence meant we personally contacted an expert for their opinion of the species’ diet.

Statistical analyses

To analyze which habitats are utilized by the most crop-pollinating Diptera larvae, we created an incidence matrix of 35 habitats (columns) and the 254 fly larvae (rows) occupying those habitats (Davis et al., 2023). The flies classified as living in the controlled conditions of a laboratory were not included in this analysis because this habitat is not naturally occurring. We created a presence/absence matrix with 1 indicating a particular species was found utilizing a habitat and 0 indicating no evidence. Using the *bipartite* package in R (Blitzer et al., 2012), we used the nestedness temperature (T) metric to determine species-specific larval habitat nestedness of the

community. This package reorganizes the presence/absence matrix by arranging habitats (columns) in the order of decreasing number of species (rows) utilizing the habitat and vice versa, therefore, maximizing nestedness in the matrix. We acknowledge that there may be a potential sampling bias towards generalist species, or easily identifiable species (Vázquez & Aizen, 2006), however, we were limited by the number of flies identified to species-level in the literature for this analysis.

To assess the non-randomness of nestedness patterns (using checkboard units) in the community, we built three null models using the *oecosimu* function in the *vegan* package in R to contrast the recorded values from the literature with randomized distributions of nestedness values to correct for type 1 or type 2 statistical errors (Selva & Fortuna, 2007; Ulrich & Gotelli, 2007). The first model “r00” maintained the recorded number of presences in the matrix, but completely randomized the species-habitat distributions. The second model “r0” maintained the species (rows) presences within the matrix but randomized the habitat distributions. The third model “c0” maintained the habitat (column) presences in the matrix but randomized the species distributions. We constructed 99 simulated null communities for each method to test against the recorded larval habitats utilized by crop-pollinating fly species.

RESULTS

Diet and habitat literature search

We found the larvae of 242 crop-pollinating flies were recorded feeding on 37 natural, 21 semi-synthetic, and 3 synthetic substrates (Appendix S1: Table S3). All natural feeding substrates utilized by both larval and adult developmental stages comprised 10 possible feeding guilds (Appendix S1: Table S3). For species utilizing natural feeding substrates, we discovered 99% of species contributed to multiple ecosystem functions as larvae (Table 1). The predatory feeding guild was utilized by the greatest number of species, with 28% of species feeding on aphids and the remainder feeding on insect eggs and/or larvae. In contrast, only four of the 242 species were thought to be fungivores in their life cycle.

For adult Diptera, differences between sexes also played an important role in governing differences in diet needs. Adult female flies in the families Calliphoridae, Fanniidae, Muscidae, Tabanidae, and Sarcophagidae were recorded using animal protein and blood to start the reproductive process of oogenesis, also known as reaching sexual maturity, while males of these 14 species fed exclusively on floral nectar. Adult female flies were also found to feed on other protein-rich substrates such as bodily fluids, and

TABLE 1 Potential ecosystem functions and inferred feeding guilds of crop-pollinating Diptera ($n = 242$) based on the feeding substrates (diets) of the flies as recorded from the literature.

Potential ecosystem function	Feeding guild	Feeding substrate(s)	Life stage	Number of families	Number of species
Decomposition	Coprophage	Manure/feces	Larva	12	40
Decomposition	Coprophage	Manure/feces	Adult	1	1
Decomposition	Detritivore	Algae, dead insects, decaying organic and plant materials, decaying seaweed, decaying fruits and vegetables, detritus, food waste, leaf litter, microorganisms, and oil waste	Larva	12	73
Decomposition	Detritivore	Decaying fruit and microorganisms	Adult	1	1
Indeterminate	Fungivore	Fungi/yeasts	Larva	3	4
Indeterminate	Fungivore	Fungi/yeasts	Adult	2	3
Pathogen (disease vector)	Hematophage	Blood	Larva	1	3
Pathogen (disease vector)	Hematophage	Blood	Adult	4	12
Herbivory	Herbivore	Cereals (crops), fruits and vegetables, plant bulbs, plant leaves (including semi-aquatic), roots and stems, and seedlings	Larva	10	30
Decomposition	Necrophage	Animal protein, bodily fluids (not blood), and carrion	Larva	7	40
Decomposition	Necrophage	Animal protein ^a and bodily fluids (not blood)	Adult	4	12
Pathogen (disease vector/ parasitism)	Parasite	Living animal tissue	Larva	6	18
Pathogen (parasitism) or Predation	Parasitoid	Living invertebrate tissue	Larva	7	25
Pollination	Pollinivore and/or nectarivore	Pollen	Larva	1	2
Pollination	Pollinivore and/or nectarivore	Pollen, nectar, orchid hair tufts, and hemipteran honeydew	Adult	32	405
Predation	Predator	Aphids, insect brood, insect eggs, other dipteran larvae, small coleopteran larvae, small hemipterans (not aphids), and small lepidopteran larvae	Larva	5	79
Predation	Predator	Other dipteran adults	Adult	3	3
Indeterminate	Unclear	Artificial diets	Larva	12	34
Indeterminate	Unclear	Artificial diets	Adult	1	1

^aAnimal protein was used by adult, female flies only.

some species are not restricted to animal protein and blood meals to achieve sexual maturity (Hickman et al., 1995; Weldon & Taylor, 2011). For example, the common house fly, *Musca domestica* Linnaeus, 1758 (Muscidae), was recorded feeding on an artificial diet of predominantly ruminant blood as an adult in laboratory settings (Roffeis et al., 2017), but we did not find records of this fly actively taking blood in natural conditions.

The larvae of 254 crop-pollinating flies live in 28 natural and 6 human-modified habitats, or in artificial habitat

within laboratory conditions (Appendix S1: Table S2). Of these species, 61.5% lived in natural habitats, 0.5% lived in human-modified habitats only, 10% were reared only in artificial habitat, and 28% lived in both artificial and natural conditions. The natural habitat that hosted the greatest number of larval species was on a host plant (either a crop or non-crop), but the habitat that hosted the greatest family diversity was artificial within the controlled conditions of a scientific laboratory (Figure 1). Under laboratory protocol, 97 species in 14 families have

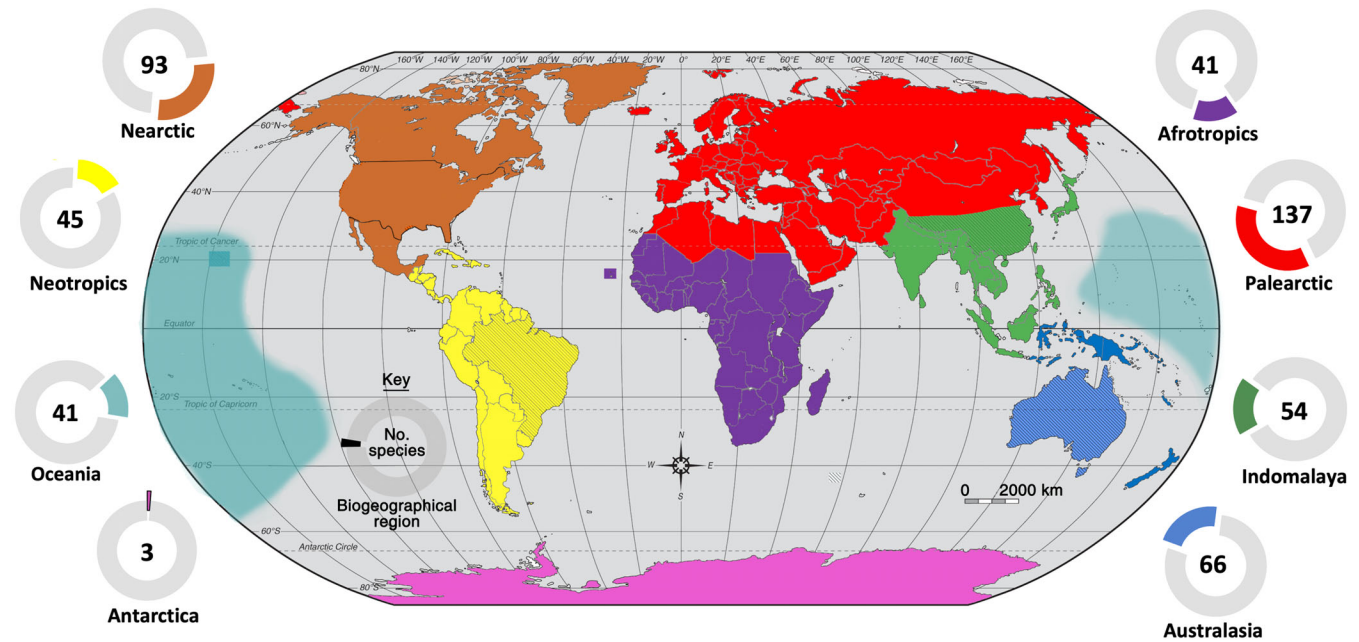


FIGURE 2 Global geographic ranges of crop-pollinating Diptera ($n = 235$) based on biogeographical region.

three cosmopolitan species, *Delia antiqua* (Meigen, 1826) (Anthomyiidae), *Fannia canicularis* (Linnaeus, 1758) (Fanniidae) and *M. domestica*, have been introduced and naturalized. Excluding the Antarctic, the family Syrphidae had the most representatives identified to species-level in all biogeographical regions except the Neotropics, where only 17 species of syrphids were identified as pollinators. Additionally, we found 117 species were endemic to one biogeographical region only, while 4% of species representing nine Diptera families were considered cosmopolitan since they inhabited six or more biogeographical regions globally.

Determining ecological feeding guilds and processes

Excluding Dipterans with unknown feeding guilds, the larvae of 242 fly species fed on substrates which were categorized into 10 different feeding guilds. Designating ecosystem services or disservices associated with fly species is beyond the scope of our study, as service/disservice delivery is dependent on environmental context; therefore, the 10 feeding guilds likely contribute to five different ecological functions, including pollination, decomposition, herbivory, potential pathogens, and predation (as seen in Table 1). The two feeding guilds that comprised the greatest number of species was the predators and the detritivores, at 79 and 73 species, respectively (Figure 3). Detritivores utilized the most generalized resources to complete their larval development, including

17 different habitats and 12 different feeding substrates. Dipteran parasitoids and pollinivores, by contrast, utilized the most specialized resources as larvae, with only one feeding substrate/habitat each. Although all adult flies fed on nectar and/or pollen, 31 species were found to feed on additional resources as adults which were categorized into seven supplementary feeding guilds (also seen in Figure 2).

We further combined the known larval and adult feeding guilds for each species to determine the full range of possible feeding guilds utilized by each fly species. We found 78% of the 242 flies used two different feeding guilds in their life cycle, feeding on one substrate as larvae and a different substrate as an adult (Figure 4). In contrast, one species, *Toxomerus floralis* (Fabricius, 1798) (Syrphidae) was found to feed on only pollen in both feeding stages, and thus was classified as having the same feeding guild in both larval and adult developmental stages. Three species, *Chrysomya megacephala* (Fabricius, 1794) (Calliphoridae), *Lucilia sericata* (Meigen, 1826) (Calliphoridae), and *M. domestica* use resources from one of six possible feeding guilds recorded for these species. For example, the blowfly *L. sericata* can survive feeding on animal protein (Daniels et al., 1991), food waste (Parry et al., 2020), living animal tissue (Demaj et al., 2020), manure/feces (Parry et al., 2020), and an artificial diet composed predominately of animal blood as larvae (Tomberlin et al., 2012; Wall et al., 2002), thus making this fly a potential necrophage, detritivore, parasite, coprophage, and hematophage in its larval stage, respectively. When the fly is an adult, however, it also feeds on

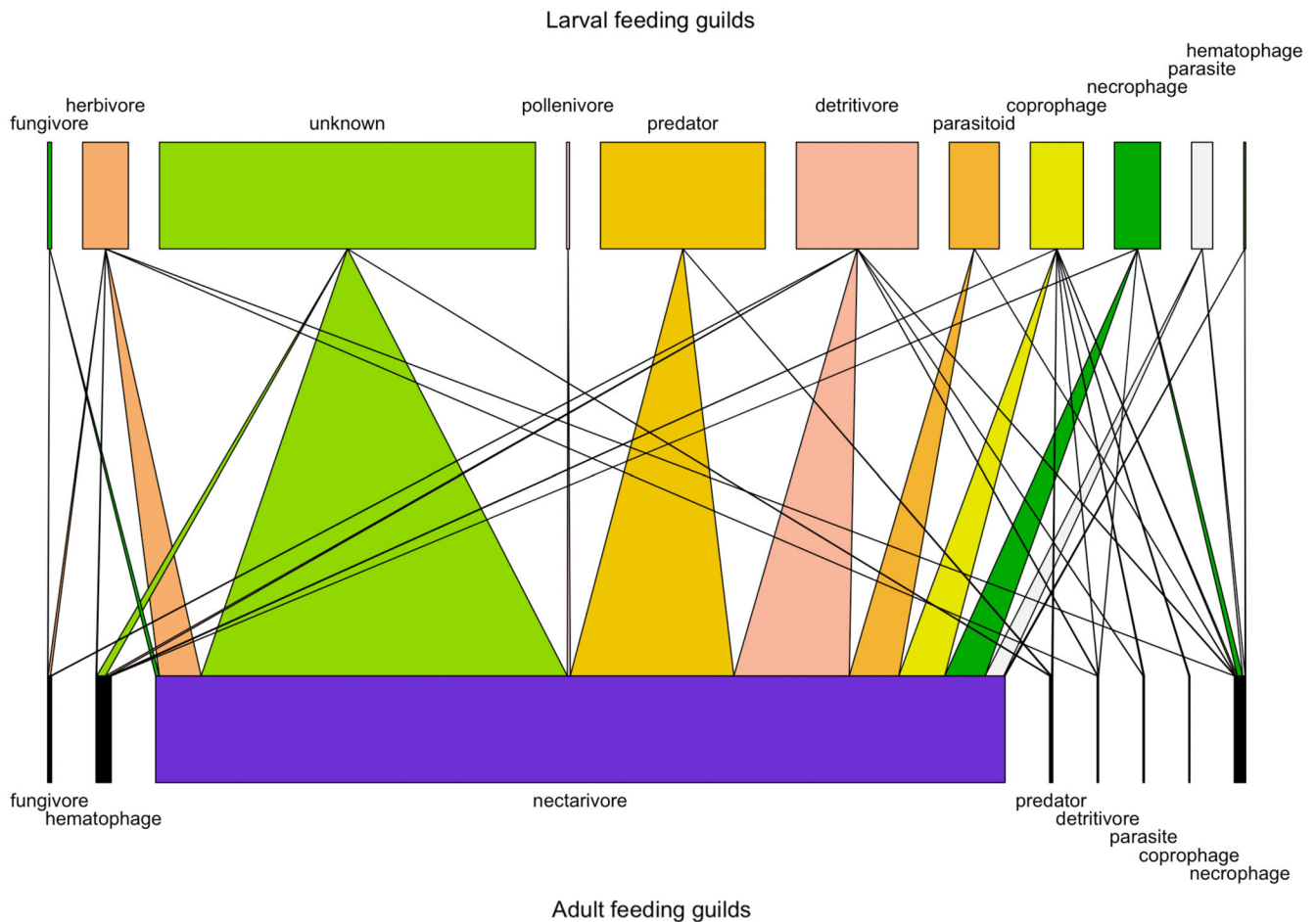


FIGURE 3 Feeding guilds of crop-pollinating fly species ($n = 405$). The width of each node is the number of species in the larval or adult stage of development that occupies a particular feeding guild, and the total node width is all 405 species searched. The node strength for each species is one, therefore the interactions are weighted to include all possible feeding guilds utilized throughout the lifecycle of each fly.

nectar and/or pollen and, therefore, is also a pollinivore/nectarivore.

Furthermore, we found 98% of the 242 species belong in different feeding guilds as larvae and adults. The remaining five of the 242 species, however, did feed on substrates which classified them as being in the same feeding guilds in both feeding stages. For example, as an adult, *Coenosia tigrina* (Fabricius, 1775) (Muscidae) preys on other adult Diptera, while (Drummond et al., 1989) observed that *C. tigrina* larvae preyed upon earthworms, thus making both larvae and adults predators. Likewise, *Toxomerus politus* (Say, 1823) (Syrphidae), was observed feeding on pollen (Nunes-Silva et al., 2010; Reemer & Rotheray, 2009), caterpillar eggs (Jirón-Pablo et al., 2018), and plant leaves as larvae (Reemer & Rotheray, 2009), thus making it a pollinivore, predator, and herbivore, respectively. Since the adult stage of *T. politus* also feeds on pollen, the two life stages of this fly share a feeding guild, although it has the potential to utilize three feeding guilds to complete its life cycle.

Reliability of larval diet information

As feeding guilds of the feeding stages of these Diptera pollinators were based on the specific feeding substrates, we also recorded which data containing the larval and adult diet information was inferred or validated by experimental, observational, or expert evidence. For all 10 larval feeding guilds, no guild was entirely comprised of species with validated dietary evidence (Appendix S2: Figure S2). Of the 1161 total data records included in our search for diet information, we found 59% of the specific larval feeding substrates were validated, 37% were inferred by authors, 2% were validated by the opinion of an expert, and 2% were unable to access. Therefore, the feeding substrates of 172 of the 242 species were validated by either experimental, observational, or expert evidence, while the feeding substrates of 62 species were entirely inferred by authors from the literature. The larval feeding substrates for six species were

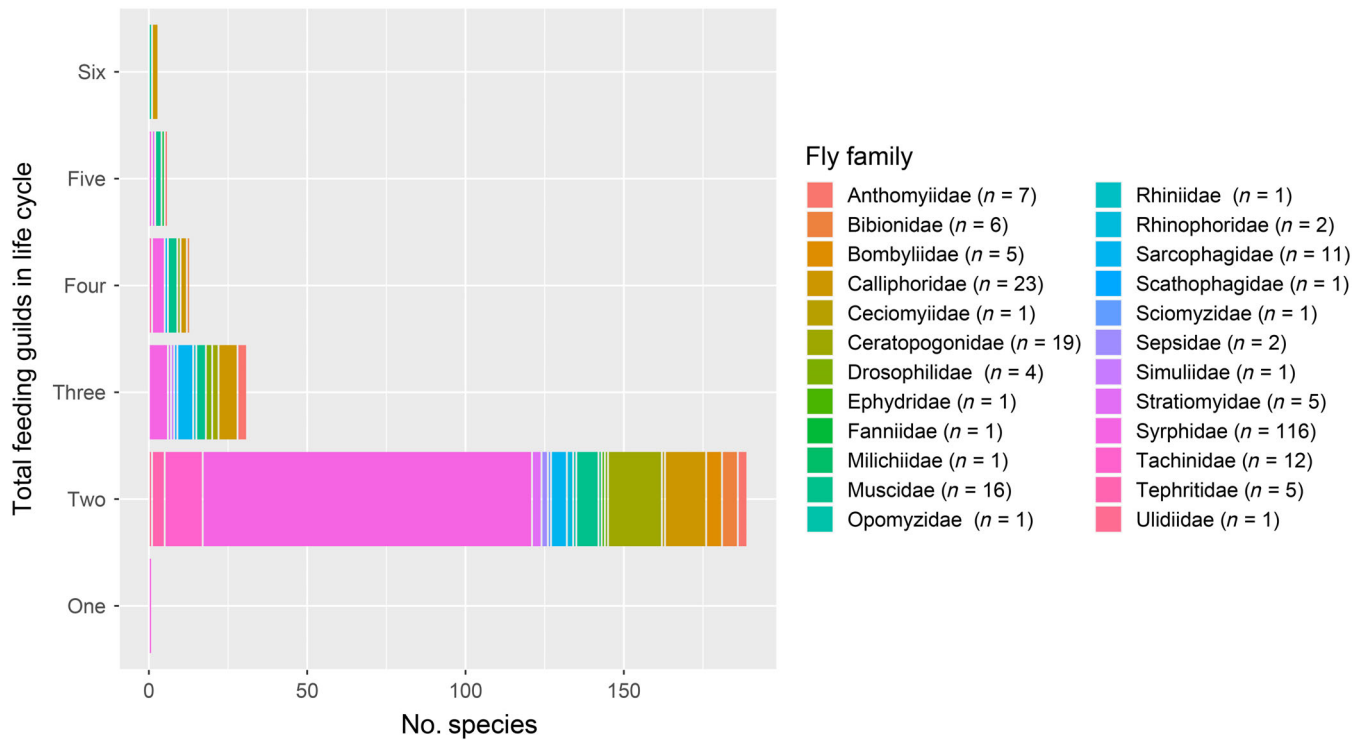


FIGURE 4 Total number of feeding guilds crop-pollinating fly species ($n = 242$) may occupy in both larval and adult life stages. Species that occupy three or more feeding guilds can (i) utilize multiple diet substrates as larvae to reach adulthood, or (ii) feed on an additional substrate to floral nectar and/or pollen as an adult.

collected from the abstracts of articles we were unable to completely access.

DISCUSSION

To meet the growing demand for pollinator-dependent agricultural food production (Tilman et al., 2011; Zabel et al., 2019), pollinators other than bees are now being recognized as important contributors and stabilizers of crop-pollination service delivery (Cook et al., 2020; Rader et al., 2016, 2020). Here we support the theory that, unlike bees, Diptera pollinators globally require different feeding substrates and habitats to support both larval and adult life stages (Truman & Riddiford, 1999). We found that of the 405 Diptera species that visit global food crops, the larvae of 254 species live in 35 different habitats, belong to 10 different feeding guilds, and inhabit all eight biogeographical regions. Very few species (2%) belonged to the same feeding guild in both feeding stages. This variability among fly life histories demonstrates that fly biodiversity conservation requires a range of resources from different habitats to support their life cycles.

Diet and habitat diversity has important implications for conservation, management, and ecosystem services. Crop flower-visiting insects are generally associated with

the pollination services they provide; however, 99% of the fly species searched in this study contributed to additional ecosystem services because they belonged to two to seven different guilds depending on how they completed their life cycles. Although this study examined only the diets and habitat needs of larval and adult crop-pollinating flies, the ecosystem services we infer here are likely a gross underestimate of the total services flies contribute to considering (1) flies and other insects are difficult to taxonomically identify and are commonly overlooked in biodiversity sampling (Troudet et al., 2017), (2) geographical sampling biases favor more accessible regions (Reddy & Dávalos, 2003), (3) the likely diversity of life history strategies across a range of natural and modified land use types and contexts (Stavert et al., 2018), and (4) the unknown life history and ecosystem functions of the remaining fly species that do not visit crop flowers (Marshall, 2012).

Our nestedness analysis suggests that generalist flies use a broad range of habitats, both natural and human-modified, for feeding and reproduction, while specialist flies only use a subset of these habitats. We found that 61.5% of fly species were recorded living in natural habitats as larvae, with the greatest number of species being detritivores or predators associated with plants, decaying plant and organic materials, and manure/feces. Although

pollinating flies with predatory larvae are beneficial in cropping systems in need of biological control services (Dunn et al., 2020; Van Oystaeyen et al., 2022), the morphological features of these flies as adults (e.g., small body size with little to no hairs to trap pollen) may make them less efficient pollinators compared to other taxa (Stavert et al., 2016). In contrast, generalist flies that are detritivores as larvae and nectarivores as adults (such as many species in the families Syrphidae, Calliphoridae, and Muscidae), make effective pollinators. They are often like honeybees in size and body hairiness (Cook et al., 2020; Stavert et al., 2016), and are capable of laying hundreds of eggs as soon as a suitable resource is available (Greenberg & Szyska, 1984; Lee & Toyamai, 1990; Nicholas et al., 2018). This capacity to adapt to resource pulses is important in agroecosystems as it suggests that many fly life histories may be supported by simple farm management practices, thus increasing the abundance of floral visitors in cropping systems.

While most beneficial detritivorous fly larvae can quickly adapt to resource pulses, they are semi-aquatic and need moist habitats to survive. One simple farm management intervention for growers looking to increase effective fly pollinators with detritivorous larvae during peak crop bloom could include deployment of plant material mounds (e.g., lawn clippings, whole plants intentionally removed after harvest and not needed anymore, etc.) near fields before flowering onset. This will give the plant material time to decay, thus attracting adult female flies (likely in the families Syrphidae and Calliphoridae) to locate the habitat, lay eggs within the decaying plant material, allow the larvae to develop to maturity, and emerge during bloom. It is important to note that these flies do not feed on living plant or organic materials, only those that are dead and decaying; therefore, the presence of these flies is unlikely to harm any part of the crop plant itself.

Howlett & Gee (2019) observed that the syrphid fly *Eristalis tenax* (Linnaeus, 1758), a species with demonstrated pollination success in various cropping systems (Cook et al., 2020), occurs naturally in large numbers within and nearby effluent ponds. For growers with property that borders livestock industries, purposefully planting crops near these facilities could increase fly pollination services and community diversity (Fijen et al., 2022; Finch et al., 2023). Additionally, when growers maintain farm landscape features, such as native plantings, open water channels, and hedgerows, crops can benefit from boosted pollination services by beneficial, wild flies and bees. For example, when pak choi (*Brassica rapa* subsp. *chinensis*) crops were grown near landscape features in New Zealand agroecosystems (e.g., effluent ponds), crop flowers received more visits from wild

pollinators capable of utilizing the resources provided by nearby landscape features in their larval stage of development (Fijen et al., 2022). This suggests that removing landscape features from agroecosystems can also remove potential pollinator habitat, which risks the loss of pollination services to nearby crops. However, the risks and benefits of maintaining landscape features within agroecosystems must first be evaluated given the possibility that some non-target species could also benefit from the landscape features and be potential pests to other crops and livestock nearby (Garratt et al., 2011; Steelman, 1976).

While these management suggestions are relevant to growers globally, different species of pollinating flies are present in different biogeographical regions, and we recognize that there is still geographical sampling bias within our data. Of the flies with known diet and habitat information, less than 45 species each were found inhabiting the Neotropical, Oceania, and Afrotropical regions, despite these regions containing some of the most biodiverse landscapes in the world (Groombridge & Jenkins, 2002; Kingsford et al., 2009). Reddy & Dávalos (2003) determined that the location and intensity of biodiversity collection and sampling efforts in the Afrotropic are heavily influenced by the physical and sociological accessibility of the region, and these results likely explain the lack of Diptera species collected and identified within the Oceania and Neotropical regions, too. As small-scale growers within these regions are most likely to benefit from the cost-effective management practices proposed here, we suggest increasing engagement with local communities and potentially implementing knowledge-sharing networks with local growers and insect taxonomists to (i) identify more beneficial fly species within these regions and (ii) suggest regional management practices tailored to local growers' needs.

More than a third of species ($n = 151$) were data deficient and only 42% of the evidence used to infer feeding guilds were validated either observationally or experimentally. While this study is limited to crop-pollinating flies, the habitat and diet needs for other pollinator taxa besides Diptera is likely similar, in that their larval stages may be providing other essential services in addition to crop pollination service delivery. Greater efforts are required to document the feeding substrates and habitats required by both larval and adult life stages of all taxa of pollinator species globally, so habitat intervention schemes and management practices support ecosystem services delivery by diverse pollinator communities and conserve them in varied landscapes. However, it is not common knowledge that taxa other than bees contribute to pollination services in society, usually due to biased coverage from mass media articles (Smith & Saunders, 2016). Therefore, future policy

intended to support and conserve non-bee pollinators must anticipate questions and possible concerns by the public to raise awareness regarding the benefits of all pollinating taxa within landscapes.

Conclusion

This paper provides new evidence that important Diptera (true flies) crop pollinators depend on diverse non-floral diets and habitat resources to complete their life cycles. We surveyed 254 world-wide fly species known to visit and potentially pollinate crop flowers as adults and found that their larvae are reared from 28 different natural habitats, 6 human-modified habitats, and feed on 36 different natural substrates. Only 2% of these species belonged to the same feeding guild in both adult and larval feeding stages, and 99% provided multiple ecosystem services in both feeding stages of development. Our research suggests that the placement of cost-effective substrates easily incorporated into mixed farming systems have the potential to increase general pollinator diversity by supporting Dipteran larval stages. We contend that current agri-environmental pollination schemes focus primarily on bees, while neglecting the importance of other pollinating insect taxa, especially Diptera. Conservation strategies to increase pollinator diversity in farmland need to consider the resource needs of the non-bee pollinator community.

AUTHOR CONTRIBUTIONS

Conceptualization (Abby E. Davis, Romina Rader), methodology (Abby E. Davis, Daniel J. Bickel, Manu E. Saunders, Romina Rader), validation (Romina Rader), formal analysis (Abby E. Davis), investigation (Abby E. Davis, Daniel J. Bickel), resources (Abby E. Davis, Daniel J. Bickel, Manu E. Saunders, Romina Rader), data curation (Abby E. Davis), writing—original draft preparation (Abby E. Davis), writing—review and editing (Abby E. Davis, Daniel J. Bickel, Manu E. Saunders, Romina Rader), visualization (Abby E. Davis), supervision (Romina Rader), project administration (Romina Rader), and funding acquisition (Romina Rader).

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CONFLICT OF INTEREST STATEMENT


The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The crop-pollinating Diptera diets and habitat needs database and novel code (Davis et al., 2023) are available in Zenodo at <https://doi.org/10.5281/zenodo.7827128>. Data utilized for this research (fly species that visit crop flowers) are freely available in Rader et al. (2020) at <https://doi.org/10.1146/annurev-ento-011019-025055> and in Allen-Perkins et al. (2022) at <https://doi.org/10.1002/ecy.3614>.

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SUPPORTING INFORMATION

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

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