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# Dual ecosystem services of syrphid flies (Diptera: Syrphidae): pollinators and biological control agents

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## Abstract

With increasing worldwide pressure on bee pollinator populations and an increase in insecticide resistance amongst pest insects, there is a growing need for diversification of pollinator and pest control systems. Syrphid flies (Diptera: Syrphidae) contribute ecosystem services to agroecosystems through their supporting roles as crop pollinators and predators of pests. Adult syrphids are important pollinators with high floral visitation rates and pollen carrying capacity, while predatory syrphid larvae are natural biological control agents, reducing aphid populations in both field and laboratory conditions. The present challenge is to determine whether syrphid flies have the potential for application as pollinators and in integrated pest management schemes as biological control agents. Currently, there are gaps in research that are hindering the use of syrphids as dual service providers. Such gaps include a lack of knowledge of syrphid floral preferences, the role and viability of adult syrphids as pollinators in natural and agro-ecological pollinator networks, and the predatory efficiency of larvae in field and glasshouse conditions. By reviewing relevant literature, we demonstrate syrphid flies have the potential to be used as pollinators and biological control agents.

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Supporting information may be found in the online version of this article.

**Keywords:** flower flies; hoverflies; pollination; aphid control; integrated pest management

## 1 INTRODUCTION

Pollination and pest control are two critical services provided by insects in natural and agricultural ecosystems. In 2012, crop pollination specifically performed by insects was estimated to produce USD\$361 billion worldwide.<sup>1</sup> However, there is considerable doubt in regards to the precision of these figures.<sup>2</sup> Regardless of economic value, approximately 35% of crops depend upon insects for some or all of their pollination needs.<sup>3</sup> At the same time, farmers spend billions of dollars controlling insect pests in their crops; these expenditures would be at least one-order of magnitude higher if natural enemies did not keep pests below economically damaging thresholds.<sup>4</sup>

Despite the massive economic value of insect pollination and natural enemies, there is increasing evidence that insect populations, including critical agricultural pollinators such as wild bees, are declining worldwide.<sup>5</sup> The reduction of insect populations and the critical services they provide are often attributed to agrarian intensification, agrochemical pollutants, landscape fragmentation and climate change.<sup>5</sup>

It is vital to understand and maintain the ecosystem services that insects provide, and to promote the growing need to replace insecticides with natural enemies and parasitoids. Traditionally, research has focused on species that excel at the provision of a single service (e.g. honeybees for pollination or parasitoid wasps for pest control). While this approach is useful, it may be more efficient to investigate species capable of simultaneously rendering

multiple services. Syrphid flies (Syrphidae: Diptera) are among the better-known dual service providers.<sup>6</sup>

Syrphids, commonly known as hoverflies or flower flies, make up one of the largest families of true flies. The family has 6674 species in 284 genera, with most species distributed in the Neotropical, Nearctic and Palaearctic regions of the world.<sup>7</sup> The distribution of syrphids is global with the exception of Antarctica and some remote oceanic islands.<sup>8</sup> Adults of most species of syrphids are flower visitors, where they feed on pollen, nectar, or both.<sup>9</sup> Several of these flower-visiting dipterans are recognized as essential pollinators in natural and agricultural systems.<sup>10,11</sup> Syrphid larvae, however, are predatory in their feeding behaviour. The larvae of three of the four Syrphidae subfamilies – Syrphinae, Pipizinae and Eristalinae (Eristalinae to a lesser extent) – are

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important predators of aphids (Aphidoidea), and other soft-bodied arthropods including thrips (Thysanoptera) and caterpillars (Lepidoptera) (Fig. 1)<sup>12</sup>

The predatory nature of syrphid larvae has encouraged investigation into the potential for syrphids to be used as a part of an integrated pest management (IPM) regime. IPM regimes aim to integrate numerous pest management strategies to reduce pesticide use and pest damage. A main component of IPM is using biological control, which entails the promotion of natural enemies (i.e. syrphid larvae) to predate or parasitize pests (i.e. aphids). While biological control will not achieve total suppression of the pest in question, the main goal is to reduce pest damage to below the economic injury threshold.<sup>13</sup>

In this review, we discuss the strengths, weaknesses and potential of using syrphids to provide both pollination and biological control services as part of an integrated IPM scheme. We also identify research gaps and make suggestions for future studies.

## 2 LARVAL SYRPHIDS AS BIOLOGICAL CONTROL AGENTS

One sustainable solution for the pest management crisis is to use natural enemies as biological control agents. Natural enemies are capable of coevolving with the pest and can respond effectively to pest population dynamics.<sup>6</sup> For example, in US agricultural systems, naturally occurring insect predators and parasitoids provide an estimated USD\$4.5 billion of pest management services each year,<sup>4</sup> through reductions in crop loss and savings from reduced insecticide use.

Predatory syrphid larvae are potential candidates for the biological control of pests such as aphids. Aphids cause significant economic damage to the world's food production industries<sup>14</sup> and are a difficult pest to manage because they occur at high densities and have rapid generation rates.<sup>15</sup> Aphid colonies are temporary,

and their locations can be unpredictable, which makes them difficult for generalist predators to find.<sup>15</sup>

One-third of all syrphid species have aphidophagous (aphid predating) larvae, and several of these species' adults have specialized aphid-finding adaptations (such as identifying prey pheromones), and as such make aphidophagous syrphids potential biological control agents for aphids in agricultural systems.<sup>16,17</sup>

For a predator to be an active biological control agent, it should be suitable for the particular environment and be able to control its prey population size (thus limiting plant injury).<sup>18</sup> The *functional response* defines the voracity and rate at which predators attack prey; this is a decisive factor in predator-prey population dynamics.<sup>19</sup> Factors such as temperature, competition, prey availability and syrphid developmental stage influence the functional response of syrphid larvae.<sup>20</sup>

### 2.1 Factors influencing the performance and voracity of syrphids

#### 2.1.1 Performance under laboratory conditions

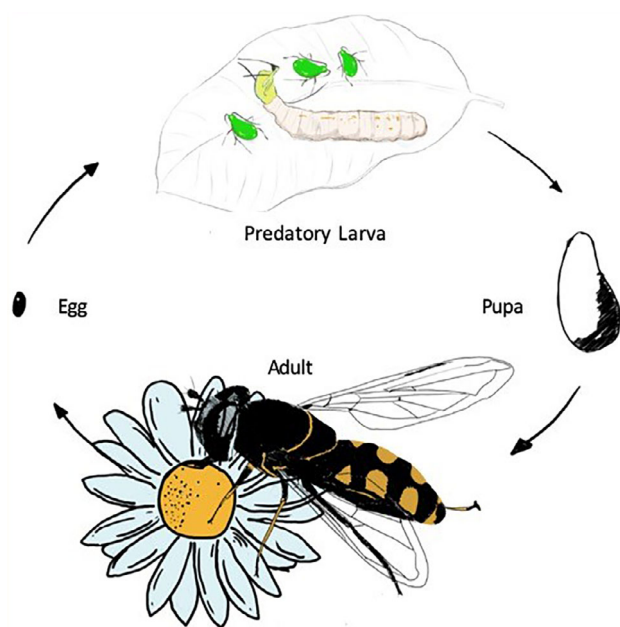
Life stage and aphid density drive the voracity of aphidophagous syrphid larvae. In general, the third larval stage – third instar – is the most voracious.<sup>16,19</sup> Larval voracity also increases with aphid density, which is a useful feature as it might allow syrphid larvae to match prey consumption rates to changes in aphid population density.<sup>21</sup> Under laboratory conditions mimicking the short cropping cycle of a lettuce crop, several syrphid species native to the United States were found to consume between 132 and 502 lettuce aphids (*Nasonovia ribisnigri*), with a daily maximum of 168 lettuce aphids being consumed per day by *Eupeodes fumipennis*.<sup>22</sup>

Temperature influences the aphid-consumption rate of syrphid larvae with optimal aphid predation occurring between 15 and 20 °C.<sup>18</sup> The effect of temperature is species-specific, explaining the range of optimal temperature. The voracity of two species, *Melangyna viridiceps* and *Symosyrphus grandicornis*, increased with temperatures up to 20 °C; once at this temperature, third instar larvae only consumed up to 80% of the total. However, *Melangyna viridiceps* consumed more aphids than *Symosyrphus grandicornis* at 10 and 15 °C. Larval development time was shorter at temperatures over 23 °C, so overall, larvae reared at higher temperatures consumed fewer aphids than larvae reared at a lower temperature.<sup>18,23</sup> These seemingly contradictory results highlight the necessity of considering the effect of environmental variables over the entire larval period. Understanding the effect of temperature on predatory efficiency is crucial to the effective deployment of syrphids in a range of crop environments.

#### 2.1.2 Performance under field conditions

Despite encouraging laboratory results, few field and glasshouse studies have demonstrated a direct reduction of aphid numbers as a result of syrphid predation.<sup>24</sup> Instead, most studies use the presence of syrphid eggs or adults as a proxy for predation<sup>21,25</sup> under the assumption that a higher density of syrphids necessarily results in lower pest numbers. Of more concern, several studies have found that the number of syrphids in a field is too low or too variable to reduce pest numbers effectively.<sup>26–29</sup> Given their efficacy under laboratory conditions, why have in-crop studies generally failed to find evidence of aphid suppression by syrphids?

One possible explanation for the lack of evidence of syrphid larval efficacy under field conditions stems from the fact that syrphids are rarely the only predators within a system. Competition between predators can powerfully affect their ability to control insect pests if one predator feeds on another, a phenomenon



**Figure 1.** The life cycle of aphidophagous syrphids. Gravid females prefer to lay eggs on plants with aphid infestations. As soon as they emerge, syrphid larvae feed on aphids. After pupation, adult syrphids shift from a predatory diet to feeding on nectar and pollen from flowers.<sup>13</sup>

known as intraguild predation or hyperparasitism. Asian lady beetles (*Harmonia axyridis*) and mirid bugs (*Macrolophus caliginosus*) are two examples of predators within the aphidophagous guild. Adults and larvae of *H. axyridis* predate on *Episyrphus balteatus* larvae even when the extraguild prey *Acyrtosiphon pisum* is present in the system.<sup>30</sup> Adult mirids, (*Macrolophus caliginosus*), predated 100% of the eggs of the syrphids *Sphaerophoria rueppellii*, *Sphaerophoria scripta*, and *Episyrphus balteatus* upon 48 h of exposure on Mediterranean vegetable crops.<sup>31</sup>

The presence of ants also reduces the predatory performance of syrphid larvae and reduces oviposition by syrphid females.<sup>32</sup> As a result, the presence of lady beetles, mirids, ants or other predators will most likely lower the efficiency of aphidophagous hoverflies in controlling aphids.<sup>32</sup>

Adult syrphid females may have behavioural strategies that can reduce the risk of intraguild predation. Females avoid laying eggs close to the eggs of other syrphids, mummified aphids or other aphid predators.<sup>16,22</sup> For example, the probability of finding *Parasyrphus* syrphid eggs declined as the densities of two predatory mirid larvae increased.<sup>33</sup> It should be noted, however, that this decrease can also be attributed to mirid larvae eating the eggs of syrphids.<sup>33</sup>

Even though some predators inhibit each other's performance, other predator combinations can have an additive effect, reducing populations more drastically when occurring together. For example, the syrphid *Episyrphus balteatus* reduces rose apple aphid (*Dysaphis plantaginea*) populations more when used in combination with the common earwig (*Forficula auricularia*).<sup>16</sup> Unfortunately, relatively few experimental studies study the impact of syrphids when combined with other biocontrol agents. More laboratory and field experiments are needed to assess which combination of aphid-predators are most efficient for controlling aphid infestation in different plants.

To some extent, adult female syrphids optimize the number and quality of their offspring by carefully choosing the best larval environments. Gravid females use their mouthparts to detect the presence of honeydew,<sup>34</sup> and prefer to oviposit on sites with higher aphid density,<sup>22,27</sup> while laying fewer eggs on plants lacking aphids.<sup>35</sup> From an IPM perspective, this is a useful characteristic as it allows females to minimize the impact of suboptimal larval microhabitats within crops.

Adult female syrphids are skilled decision-makers using factors such as the nutritional value and density of the aphids present, the predation risk associated with the site, competitive pressure from other aphid predators and quality of the host plant to determine the quality of oviposition site in regards to optimum offspring survival.<sup>36</sup>

The decision-making ability of syrphids has largely been determined through both field and laboratory studies where syrphid species are exposed to a range of potential oviposition stimuli to establish oviposition preferences and triggers. For instance, the presence and absence of aphids (*Aphis fabae* Scop.) on potted bean plants (*Vicia faba* L.), was used to test aphid colony presence as an oviposition stimulus for a variety of syrphid species.<sup>37</sup> All but one species of syrphid showed no effective response (i.e. chose not to oviposit) to plants uninfested with aphids. Moreover, syrphids were not deterred from ovipositing on suitable plants infested with aphids in the presence of other syrphid eggs, syrphid larvae or larval gut contents.<sup>37</sup>

The fact that syrphids typically occur at low population densities is another potential reason for the lack of aphid suppression in field studies. A shortage of the nectar and pollen required for

adult nutrition is a possible constraint.<sup>38</sup> Adult syrphids use nectar as an energy source and rely on pollen to complete their reproductive cycle.<sup>6</sup> Given the importance of flowers for syrphid maintenance and reproduction, inadequate floral resources – for adults – or alternative prey – for larvae – could explain low syrphid population numbers in the wild. Supplying extra floral resources or artificial diets (i.e. sugar water) to attract adult syrphids to an area is a possible solution that requires more research.<sup>28,39</sup>

Recent field studies have focused on attracting syrphid adults into crops by planting floral resources.<sup>21,40</sup> Flowers such as buckwheat (*Fagopyrum esculentum*), cornflower (*Centaurea cyanus*), alyssum (*Lobularia maritima*), coriander (*Coriandrum sativum*), and mint (*Mentha spicata*) are attractive to syrphid adults.<sup>21,25,38</sup> However, syrphid fecundity, larval density and aphid suppression were not affected when additional floral resources were grown on land adjacent to the cropped lands.<sup>21,25</sup> This may be because of the differing dietary needs of adult and larval syrphids that complicates attempts to provide a syrphid-promoting habitat.

Adult female syrphids will make a decision to oviposit in an area more suitable for the larvae over her own requirement or desire for floral resources (nectar and pollen).<sup>21,25</sup> Thus, aphid population and density, rather than floral resources available and attractive to adult females, directly affect ovipositional choice and subsequent syrphid larval density.<sup>21,25</sup> As such, if the goal is to incorporate extra floral resources to encourage adult females to oviposit, and thus benefit from the predatory larvae, then planting extra floral resources is likely not the best method. However, it would still be useful to have floral resources in surrounding habitats that are attractive to adult syrphids to encourage their presence throughout the landscape.<sup>41</sup>

While adding floral resources does not seem to influence syrphid fecundity, larval density or aphid suppression, the presence of naturally occurring resources can influence aphidophagous syrphids in the area. Surrounding landscape features such as forests, floral resource availability or landscape fragmentation can influence populations of aphidophagous syrphids in the area.<sup>41</sup> Focus has often been on the effect of landscape changes on aphidophagous syrphid species, due to their role in agricultural systems. Floral density over a landscape radius of between 500 and 1000 m positively influences abundance of aphidophagous syrphids.<sup>41,42</sup> However, an increase in flower numbers does not translate into an increased number of eggs.<sup>6</sup> These studies suggest that attempts to increase syrphid numbers in crops need to consider both larval and adult habitat preferences.

Syrphid larvae have shown great potential as aphid control agents under laboratory conditions, but several knowledge gaps remain. In particular, research on intraguild predation, syrphid dispersal and the habitat requirements of larvae and adults are needed to improve the efficacy of pest suppression under field conditions.

### 3 ADULT SYRPHIDS AS POLLINATORS

#### 3.1 Pollination ability and efficacy

We reviewed articles in which species of plants visited by syrphid flies were reported<sup>10,43–57</sup> and found records of syrphid visits on plants from 36 families (Supporting Information Figs S1 and S2). Both aphidophagous and non-aphidophagous syrphid species are typically classified as generalist flower visitors (i.e. visiting a wide range of plant species).<sup>13</sup> Syrphids in the genera *Eupeodes*, *Sphaerophoria*, *Syrphus*, *Eristalis* and *Episyrphus* visited at least 40 different species of plants, from not less than 15 families

(Figs S1 and S2). Although these five genera seem to be more generalist than many other species, this could be an artefact of the other species being studied less frequently, being less pervasive, or due to differences in the scope of the reviewed studies.

While syrphids are known to visit a broad range of plants, including many crop species, visitation alone is not sufficient to guarantee adequate pollination.<sup>58</sup> Three key components determine the pollinating ability of an insect: the number of pollen grains the insect can transport, the insect's visitation rate and the frequency of pollen deposition on the stigma of the flowers of interest.<sup>43,59</sup>

Bees can carry more pollen than syrphid flies, due to morphological traits such as hairiness and size.<sup>60,61</sup> Despite these morphological limitations, some syrphid species can carry relatively high numbers of pollen grains,<sup>61</sup> and be as effective at pollination as other insects such as wild bees and honey bees.<sup>11,59,60</sup> For example, the syrphid species *Eristalis tenax* was as likely as honey bees to touch the stigmatic surfaces when attending flowers of *Brassica rapa* var. *chinensis*, and both insects deposited a similar amount of pollen on the stigmas of virgin flowers.<sup>59</sup> However, the higher abundance of honey bees resulted in them being the more effective pollinator overall.<sup>59</sup>

Syrphids might be reducing interspecific competition by avoiding flowers preferred by other species, as revealed using DNA metabarcoding.<sup>62</sup> The pollen transport networks of the 11 species across five genera were more generalized in their structure than specialized; this means that syrphid species are transporting pollen of multiple plants and individual plants are visited by multiple syrphids.<sup>62</sup> Furthermore, although pollen loads are similar between syrphid species, pollen load composition (i.e. the main constituents of pollen loads) varies between syrphid species. Thus, syrphids may fulfil complementary roles in pollen transport.<sup>62</sup> Complementary roles, often referred to as niche differentiation or resource partitioning, is where competing species use the environment and resources differently to successfully coexist.<sup>63</sup>

For pollination to occur, the pollen deposited on the stigma of the flower must be viable. Bees often carry a higher proportion of viable pollen than syrphid flies due to bees' morphological traits such as size, body hair and pollen carrying traits such as pollen sacks on the legs.<sup>60</sup>

The distance that a pollinator travels before landing on a suitable partner plant influences the carrying capacity of viable pollen. Some Syrphidae are able to carry viable pollen a maximum of 400 m, while bees (Apidae and Halictidae) carry viable pollen only up to 300 m.<sup>60</sup> Bee species from the Apidae and Halictidae families carry more total pollen than flies from Stratiomyidae and Syrphidae families at 200 m; however, flies retained significantly more total pollen than bees at 100 m. These results suggest that syrphid flies are capable of carrying pollen effectively and might outperform honeybees (Apidae) in carrying viable pollen to greater distances. Thus, having a variety of different pollinating insects with varying dispersal rates present in an agricultural setting can promote pollen movement and gene flow through the landscape.<sup>60</sup>

Though adult syrphids are usually generalist feeders, flowers differ in their attractiveness to syrphids. The main trait that drives attractiveness is pollen and nectar accessibility. Whether or not syrphids can effectively access nectar or pollen depends on the shape of their mouthparts. Aphidophagous syrphids tend to have a short proboscis that prevents them from feeding on flowers that are tubular or have deep corollas such as broad bean (*V. faba*).<sup>64</sup> Syrphids with short probosces typically show a stronger

preference for plants with short corollas of less than 3 mm in depth and available (i.e. easily accessible through a short corolla) nectar such as coriander (*Coriandrum sativum*). Field trials suggest that corolla length is the most important flower trait that drives syrphid abundance – even more so than flower colour.<sup>38</sup> For example, *Episyrphus balteatus* and *Episyrphus corollae* (to a lesser extent) were more abundant in fields with high cover of flowers with open nectar and shorter corollas.<sup>38,40</sup>

While nectar accessibility is important to syrphids, morphological features such as corolla length, floral 'openness' and floral shape are typically only useful to attract pollinators at close range.<sup>65</sup> At a distance, some pollinating insects may not visually perceive the shape and form (i.e. corolla length) of a flower. However, floral traits such as colour may influence attractiveness from a distance.<sup>66</sup>

Syrphids are typically attracted to yellow and white flowers but colour preference can vary between species and sexes,<sup>44,45</sup> and there is limited literature available to determine preferences for the vast majority of syrphid species. Further research into flower features such as intensity, brightness, wavelength content and contrast has been suggested.<sup>67</sup> Additionally, more in-depth investigations into colour perception of flies are needed.<sup>67</sup>

In regards to colour vision stimuli for syrphid flies, a recent study has tested the psychophysics of the syrphid species *Eristalis tenax* and concluded that syrphids can distinguish two stimuli from the same colour category (e.g. two different shades of yellow), with colour discrimination being significantly greater for yellow stimuli in comparison to blue stimuli. The fact that syrphid eyes appear tuned to distinguish shades of yellow supports other studies demonstrating that syrphids have a preference for yellow flowers.<sup>44,45,68</sup>

### 3.2 Syrphids as pollinators of commercial crops

The effectiveness of syrphid pollination in agro-ecosystems has primarily been examined in horticultural plants in glasshouses,<sup>21,46</sup> with some more recent studies undertaken in field or semi-field conditions.<sup>21,69</sup> Controlled pollination experiments have shown that syrphids, predominantly *Eristalis tenax*, are useful in increasing seed production of some food crops such as onion, oilseed rape (*B. napus*), sweet pepper (*Capsicum annuum*), strawberry (*Fragaria × ananasa*), and a variety of wild plants.<sup>21,46,47</sup> For example, in a glasshouse experiment, sweet pepper (*Capsicum annuum*) plants that were visited by *Eristalis tenax* had more abundant fruit and higher seed set than the sweet pepper plants that were not visited.<sup>47</sup>

In cage trials using the solitary red mason bee, *Osmia rufa* and two syrphid species (*Eristalis tenax* and *Episyrphus balteatus*), the yield of oilseed rape positively correlated to insect density. Syrphids required densities approximately five-fold higher than that of the red mason bee to reach a similar fruit set and yield, possibly because hoverflies carry less pollen than mason bees.<sup>46,48</sup>

Unlike bees, syrphids are not central place foragers meaning that they do not return to a consistent nesting site after foraging. As a result, syrphids may respond to high pollinator densities by shifting from small-scale movements between neighbouring flowers to large-scale dispersal activities.<sup>46</sup> If so, then the effectiveness of adding syrphids to crops may be limited when there is an overall abundance of pollinators<sup>25</sup> as syrphids may respond by leaving the system. More research on syrphid dispersal is needed to address this potential shortcoming.

There is increasing interest in supporting pollinators by adding floral resources between crop rows (intercropping). However,



intercropping can backfire if the support plants attract pollinators away from the focal crop. For example, intercropping strawberry (the target crop) with coriander and mint under glasshouse conditions, resulted in insects preferentially visiting the coriander and mint plants at the expense of the strawberry crop.<sup>21,25</sup> In these studies, the numbers of syrphid larvae and eggs were positively correlated to aphid abundance but did not differ by presence or absence of additional floral resources.<sup>21,25</sup> Moreover, the marketable yield of strawberry was not increased. These results seem to indicate that intercropping may not be a good strategy for enhancing pollination and pest control by syrphids, but more research using different crops and intercrop species is urgently needed to determine the generalizability of this finding. A better understanding of how syrphids choose flowers would aid in the selection of intercrop species that support syrphids without distracting them away from focal crops.

## 4 DISCUSSION

Only a few species of syrphids have been studied in-depth, and this paucity of knowledge currently limits the inclusion of syrphids in a successful IPM strategy. Little is known about the aphid consumption rates, habitat requirements, flower preferences, and pollination potential of the vast majority of syrphid species. Since most experiments on syrphids have been conducted in laboratories, translation of findings to the crop environment is limited. Laboratory experiments do not always show a clear demonstration of what will be successful in the field<sup>22</sup> and often fail to consider environmental factors such as temperature, rainfall, humidity, competition and predation that may occur in the field.<sup>26</sup> Additional field-based and glasshouse trials are necessary to determine the efficacy of syrphids as biological control agents and pollinators.

The results of experiments focused on the pollination efficacy of syrphids in glasshouse and field environments have led to equivocal results. However, even if syrphids are not the most efficient pollinators in particular systems, attracting them can lead to an increase in overall pollinator diversity which in turn can increase fruit and seed production,<sup>70</sup> reduce the risk of pollinator dilution,<sup>71</sup> and maintain pollination services across regional scales.<sup>72</sup> Therefore, the encouragement of syrphids alongside more traditional pollinators such as honeybees is likely to improve outcomes for food production systems.

There are several ways that syrphid larvae could be introduced in the crop environment. Techniques based on 'conservation biological control' aim to attract beneficial insects through the provision of suitable habitat.<sup>6</sup> Future work should focus not just on the proximate effects of floral plantings on the number of syrphids but also on metrics relevant to producers (number of aphids, yield, and crop quality). More research is also needed to understand the nutritional needs and flower preferences of syrphid flies, as this knowledge can inform the choice of support plants within the crop.

Mass rearing and release of syrphids is another option for use in crop environments. Unfortunately, rearing predators that require both prey and floral resources across different life stages can be challenging. Several aspects of syrphid biology including nutritional requirements need to be investigated thoroughly for mass-rearing programmes to be successfully integrated into IPM strategies.

Understanding potential sources of mortality are important for the development of a mass-rearing programme. In the wild, the

leading causes of syrphid deaths are parasitoid attacks, bacterial pathogens and viral infections.<sup>73</sup> Of these, bacterial and viral infections are of the most significant concern as they can quickly destroy mass-rearing operations. Parasitoid wasps can also be problematic, mainly if they are brought in with collected syrphid larvae. Ichneumonid wasps are the principal parasitoids of syrphid larvae, although members of several other Hymenoptera families including wasp species from Pteromalidae and Encyrtidae have been identified and studied.<sup>74–76</sup> At least one study has reported syrphid larval defence mechanisms against parasitoid attacks,<sup>77</sup> though quantification of the efficiency of these actions on avoiding parasitism has not been undertaken. Whether parasitoids are likely to be a significant problem in captive rearing environments is not yet known. However, if following a mass-rearing practice, parasitoidy by wasps may be reduced by releasing syrphid larvae at third-instar only<sup>76</sup> because the feeding capacity of larvae is impacted less and the survival rate may be higher.<sup>74,75</sup>

The development of a synthetic diet would significantly increase the potential for syrphids to be used as part of an augmentative biological control strategy. Currently, there is little known about the specific nutritional requirements of syrphid larvae and adults. Some generalist soft-bodied insect feeders (e.g. lacewings) can be reared on frozen moth eggs which simplify the rearing process.<sup>39</sup> Given the potential uses of syrphids in both pest control and pollination, the development of a scalable breeding process should be a research priority.

The dietary and habitat flexibility of syrphids across spatial scales may safeguard their populations from fluctuations in food availability.<sup>78</sup> Syrphids are known to be more tolerant of land-use change than bumblebees and honey bees,<sup>11</sup> and less prone to dilution in pollinator abundance in mass-flowering crops.<sup>71</sup> This tolerance could help stabilize pollination services in places where land-use has changed, and bee pollinator populations have declined.<sup>11</sup> Additionally, most aphidophagous syrphid larvae can predate several aphid species.<sup>73</sup> Their broad dietary requirements and ability to withstand land change may make syrphids essential components in developing resilient pollination and pest control systems.

The biological differences between syrphid species (e.g. larval diet, adult diet, mobility, floral preferences, etc.), and their ability to tolerate environmental modifications suggest that syrphids have potential as providers of pollination and pest control services in different contexts. Integration of syrphids into an IPM programme requires more information on the physiological and dietary needs of syrphid species. Given the vast diversity of syrphid species, there are many opportunities to target research toward species (or combinations of species) most appropriate for particular crop plants and contexts (e.g. glasshouses, mixed cropping, broad acre).

Moreover, the inclusion of syrphids in an IPM programme will require research into the impacts of other agrichemicals such as neonicotinoid insecticides on syrphid pollination and predatory efficiency. Such information will inform the creation of best-practice guidelines that ensure syrphids are not negatively impacted by other IPM tools.

However, when the dual effect of syrphids is harnessed and their integration into IPM schemes is successful, it may provide economic incentive to consider their introduction in a place or alongside their single service providing counterparts (e.g. honey bee). The dual pollination and pest control roles of syrphids make these largely overlooked flies potentially powerful allies in the struggle to develop sustainable agriculture.

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## CONFLICT OF INTEREST

The authors have no conflicts of interests to declare.

## AUTHORS CONTRIBUTIONS

Lucinda Dunn, Tanya Latty and Chris Reid conceived the ideas and basis of the review; Lucinda Dunn and Manuel Lequerica collected the articles and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

## REFERENCES

- Lautenbach S, Seppelt R, Liebscher J and Dormann CF, Spatial and temporal trends of global pollination benefit. *PLoS One* **7**:e35954 (2012).
- Hanley N, Breeze TD, Ellis C and Goulson D, Measuring the economic value of pollination services: principles, evidence and knowledge gaps. *Ecosyst Serv* **14**:124–132 (2015).
- Gallai N, Salles J-M, Settele J and Vaissière BE, Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol Econ* **68**:810–821 (2009).
- Losey JE and Vaughan M, The economic value of ecological services provided by insects. *Bioscience* **56**:311–323 (2006).
- Sánchez-Bayo F and Wyckhuys KA, Worldwide decline of the entomofauna: a review of its drivers. *Biol Conserv* **232**:8–27 (2019).
- Omkar GM, *Syrphid Flies (the Hovering Agents)*. Academic Press, San Diego, CA (2016).
- Secretariat SiG, Gbif backbone taxonomy checklist dataset. <https://doi.org/10.15468/39omei> [accessed 5 February 2018].
- Thompson FC and Rotheray G, Manual of palaearctic diptera. *Family Syrphidae* **3**:81–139 (1998).
- Larson B, Kevan P and Inouye DW, Flies and flowers: taxonomic diversity of anthophiles and pollinators. *Can Entomol* **133**:439–465 (2001).
- Klecka J, Hadrava J, Biella P and Akter A, Flower visitation by hoverflies (diptera: Syrphidae) in a temperate plant–pollinator network. *PeerJ* **6**:e26516v26511 (2018).
- Rader R, Bartomeus I, Garibaldi LA, Garratt MP, Howlett BG, Winfree R et al., Non-bee insects are important contributors to global crop pollination. *PNAS* **113**:146–151 (2016).
- Skevington JH and Dang PT, Exploring the diversity of flies (Diptera). *Biodiversity* **3**(4): 3–27 (2002).
- Rotheray GE and Gilbert F, The Natural History of Hoverflies. Forrest Text, Cardigan, (2011).
- Blackman RL and Eastop VF, Taxonomic issues, in *Aphids as Crop Pests*, ed. by van Emden HF and Harrington R. CABI, Wallingford, pp. 1–29 (2017).
- Almohamad R, Verheggen FJ and Haubruge É, Searching and oviposition behavior of aphidophagous hoverflies (diptera: Syrphidae): a review. *Biotechnol Agron Soc* **13**:467–481 (2009).
- Dib H, Simon S, Sauphanor B and Capowiez Y, The role of natural enemies on the population dynamics of the rosy apple aphid, *Dysaphis plantaginea* passerini (hemiptera: Aphididae) in organic apple orchards in south-eastern France. *Biol Control* **55**:97–109 (2010).
- Mizuno M, Itohi T, Tatematsu Y and Ito Y, Food utilization of aphidophagous hoverfly larvae (diptera: Syrphidae, chamaemyiidae) on herbaceous plants in an urban habitat. *Ecol Res* **12**:239–248 (1997).
- Soleyman-Nezhadiyan E, The ecology of *Melangyna viridiceps* and *S. grandicornis* (diptera: Syrphidae) and their impact on populations of the rose aphid, *Macrosiphum rosae*. PhD thesis, University of Adelaide, Adelaide, (1997).
- Arcaya E, Pérez-Bañón C, Mengual X, Zubcoff-Vallejo JJ and Rojo S, Life table and predation rates of the syrphid fly *Allograpta exotica*, a control agent of the cowpea aphid *Aphis craccivora*. *Biol Control* **115**: 74–84 (2017).
- Leir V and Barlow C, Effects of starvation and age on foraging efficiency and speed of consumption by larvae of a flower fly, *Metasyrphus corollae* (syrphidae). *Can Entomol* **114**:897–900 (1982).
- Hodgkiss D, Brown MJF and Fountain MT, The effect of within-crop floral resources on pollination, aphid control and fruit quality in commercial strawberry. *Agr Ecosyst Environ* **275**:112–122 (2019).
- Nelson EH, Hogg BN, Mills NJ and Daane KM, Syrphid flies suppress lettuce aphids. *BioControl* **57**:819–826 (2012).
- Soleyman-Nezhadiyan E and Laughlin R, Voracity of larvae, rate of development in eggs, larvae and pupae, and flight seasons of adults of the hoverflies *Melangyna viridiceps* macquart and *Symosyrphus grandicornis* macquart (diptera: Syrphidae). *Aust Entomol* **37**:243–248 (1998).
- Dib H, Jamont M, Sauphanor B and Capowiez Y, Predation potency and intraguild interactions between generalist (*Forficula auricularia*) and specialist (*Episyrphus balteatus*) predators of the rosy apple aphid (*Dysaphis plantaginea*). *Biol Control* **59**:90–97 (2011).
- Gillespie M, Wratten S, Sedcole R and Colfer R, Manipulating floral resources dispersion for hoverflies (diptera: Syrphidae) in a California lettuce agro-ecosystem. *Biol Control* **59**:215–220 (2011).
- Eckberg JO, Peterson JA, Borsh CP, Kaser JM, Johnson GA, Luhman JC et al., Field abundance and performance of hoverflies (Diptera: Syrphidae) on soybean aphid. *Ann Entomol Soc Am* **108**:26–34 (2014).
- Tenhumberg B and Poehling H-M, Syrphids as natural enemies of cereal aphids in Germany: aspects of their biology and efficacy in different years and regions. *Agr Ecosyst Environ* **52**:39–43 (1995).
- Schirmel J, Albrecht M, Bauer P-M, Sutter L, Pfister SC and Entling MH, Landscape complexity promotes hoverflies across different types of semi-natural habitats in farmland. *J Appl Ecol* **55**:1747–1758 (2018).
- Meyer B, Jauker F and Steffan-Dewenter I, Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic Appl Ecol* **10**:178–186 (2009).
- Ingels B and De Clercq P, Intraguild predation between *Harmonia axyridis* and the hoverfly *episyrphus balteatus*. In *IOBC/WPRS Harmonia meeting: Harmonia axyridis and other invasive ladybirds*. International Organisation for Biological and Integrated Control of Noxious Animals and Plants (IOBC). West Palaearctic Regional Section (WPRS), Engelberg, Switzerland (2009).
- Fréchette B, Rojo S, Alomar O and Lucas É, Intraguild predation between syrphids and mirids: who is the prey? Who is the predator? *BioControl* **52**:175 (2007).
- Amiri-Jami A, Sadeghi-Namaghi H and Gilbert F, Performance of a predatory hoverfly feeding on *Myzus persicae* (hem. Aphididae) reared on two brassicaceous plants varies with ant attendance. *Biol Control* **105**:49–55 (2017).
- Björkman C, Johansson H and Snäll T, Spatial distribution of interacting insect predators: possible roles of intraguild predation and the surrounding habitat. *Basic Appl Ecol* **12**:516–522 (2011).
- Budenberg W and Powell W, The role of honeydew as an ovipositional stimulant for two species of syrphids. *Entomol Exp Appl* **64**:57–61 (1992).
- Chandler A, The relationship between aphid infestations and oviposition by aphidophagous syrphidae (diptera). *Ann Appl Biol* **61**: 425–434 (1968).
- Mangel M, Opposition site selection and clutch size in insects. *J Math Biol* **25**:1–22 (1987).
- Dixon T, Studies on oviposition behaviour of syrphidae (diptera). *Ecol Entomol* **11**:57–80 (1959).
- PCJ v R, Kooijman J and Waeckers FL, The impact of floral resources on syrphid performance and cabbage aphid biological control. *IOBC-WPRS Bulletin* **29**:149–152 (2006).
- Morrison RK, House VS and Ridgway RL, Improved rearing unit for larvae of a common green lacewing 123. *J Econ Entomol* **68**:821–822 (1975).
- Campbell AJ, Biesmeijer JC, Varma V and Waeckers FL, Realising multiple ecosystem services based on the response of three beneficial insect groups to floral traits and trait diversity. *Basic Appl Ecol* **13**: 363–370 (2012).

- 41 Moquet L, Laurent E, Bacchetta R and Jacquemart AL, Conservation of hoverflies (Diptera, syrphidae) requires complementary resources at the landscape and local scales. *Insect Conserv Diver* **11**:72–87 (2018).
- 42 Hussain RI, Walcher R, Brandl D, Aramberger A, Zaller JG and Frank T, Efficiency of two methods of sampling used to assess the abundance and species diversity of adult syrphidae (diptera) in mountainous meadows in the Austrian and Swiss alps. *Eur J Entomol* **115**:150–156 (2018).
- 43 Herrera CM, Pollinator abundance, morphology, and flower visitation rate: analysis of the “quantity” component in a plant–pollinator system. *Oecologia* **80**:241–248 (1989).
- 44 Colley M and Luna J, Relative attractiveness of potential beneficial insectary plants to aphidophagous hoverflies (diptera: Syrphidae). *Environ Entomol* **29**:1054–1059 (2000).
- 45 Haslett J, Interpreting patterns of resource utilization: randomness and selectivity in pollen feeding by adult hoverflies. *Oecologia* **78**:433–442 (1989).
- 46 Jauker F and Wolters V, Hover flies are efficient pollinators of oilseed rape. *Oecologia* **156**:819 (2008).
- 47 Jarlan A, De Oliveira D and Gingras J, Pollination by *Eristalis tenax* (diptera: Syrphidae) and seed set of greenhouse sweet pepper. *J Econ Entomol* **90**:1646–1649 (1997).
- 48 Jauker F, Bondarenko B, Becker HC and Steffan-Dewenter I, Pollination efficiency of wild bees and hoverflies provided to oilseed rape. *Agric Forest Entomol* **14**:81–87 (2012).
- 49 Ali M, Saeed S, Sajjad A and Whittington A, In search of the best pollinators for canola (*Brassica napus* L.) production in Pakistan. *Appl Entomol Zool* **46**:353–361 (2011).
- 50 Branquart E and Hemptinne JL, Selectivity in the exploitation of floral resources by hoverflies (diptera: Syrphinae). *Ecography* **23**:732–742 (2000).
- 51 Cowgill S, Sotherton N and Wratten S, The selective use of floral resources by the hoverfly *Episyrphus balteatus* (diptera: Syrphidae) on farmland. *Ann Appl Biol* **122**:223–231 (1993).
- 52 Gontijo LM, Beers EH and Snyder WE, Flowers promote aphid suppression in apple orchards. *Biol Control* **66**:8–15 (2013).
- 53 Goulson D and Wright NP, Flower constancy in the hoverflies *Episyrphus balteatus* (degeer) and *Syrphus ribesii* (L.) (syrphidae). *Behav Ecol* **9**:213–219 (1998).
- 54 King C, Ballantyne G and Willmer PG, Why flower visitation is a poor proxy for pollination: measuring single-visit pollen deposition, with implications for pollination networks and conservation. *Methods Ecol Evol* **4**:811–818 (2013).
- 55 Hodgson DJ, MacLeod A, Wratten SD and Lövei GL, Attractiveness of some novel crops for flower visiting hoverflies (Diptera: Syrphidae): comparisons from two continents, in *Pest Control and Sustainable Agriculture*, ed. by Corey SA, Dall DJ and Milne WM. CSIRO Publications, Canberra, pp. 368–370 (1993).
- 56 Stökl J, Brodmann J, Dafni A, Ayasse M and Hansson BS, Smells like aphids: orchid flowers mimic aphid alarm pheromones to attract hoverflies for pollination. *Proc R Soc Lond B* **278**:1216–1222 (2011).
- 57 Villa M, Santos SAP, Marrão R, Pinheiro LA, López-Saez JA, Mexia A et al., Syrphids feed on multiple patches in heterogeneous agricultural landscapes during the autumn season, a period of food scarcity. *Agric Ecosyst Environ* **233**:262–269 (2016).
- 58 Ne’eman G, Jürgens A, Newstrom-Lloyd L, Potts SG and Dafni A, A framework for comparing pollinator performance: effectiveness and efficiency. *Biol Rev* **85**:435–451 (2010).
- 59 Rader R, Howlett BG, Cunningham SA, Westcott DA, Newstrom-Lloyd LE, Walker MK et al., Alternative pollinator taxa are equally efficient but not as effective as the honeybee in a mass flowering crop. *J Appl Ecol* **46**:1080–1087 (2009).
- 60 Rader R, Edwards W, Westcott DA, Cunningham SA and Howlett BG, Pollen transport differs among bees and flies in a human-modified landscape. *Divers Distrib* **17**:519–529 (2011).
- 61 Phillips BB, Williams A, Osborne JL and Shaw RF, Shared traits make flies and bees effective pollinators of oilseed rape (*Brassica napus* L.). *Basic Appl Ecol* **32**:66–76 (2018).
- 62 Lucas A, Bodger O, Brosi BJ, Ford CR, Forman DW, Greig C et al., Floral resource partitioning by individuals within generalised hoverfly pollination networks revealed by DNA metabarcoding. *Sci Rep* **8**:5133 (2018).
- 63 Blüthgen N and Klein A-M, Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. *Basic Appl Ecol* **12**:282–291 (2011).
- 64 Gilbert FS, Foraging ecology of hoverflies: morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. *Ecol Entomol* **6**:245–262 (1981).
- 65 Kearns CA, Inouye DW and Waser NM, Endangered mutualisms: the conservation of plant–pollinator interactions. *Ann Rev Ecol Syst* **29**:83–112 (1998).
- 66 Lunau K and Maier E, Innate colour preferences of flower visitors. *J Comp Physiol A* **177**:1–19 (1995).
- 67 Petanidou T and Lamborn E, A land for flowers and bees: studying pollination ecology in Mediterranean communities. *Plant Biosyst* **139**:279–294 (2005).
- 68 Hannah R, Dyer AG, Garcia JE, Dorin A and Burd M, Psychophysics of the hoverfly: categorical or continuous color discrimination? *Curr Zool* **65**:483–492 (2019).
- 69 Gervais A, Chagnon M and Fournier V, Diversity and pollen loads of flower flies (diptera: Syrphidae) in cranberry crops. *Ann Entomol Soc Am* **111**:326–334 (2018).
- 70 Fontaine C, Dajoz I, Meriguet J and Loreau M, Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. *PLoS Biol* **4**:e1 (2006).
- 71 Holzschuh A, Dainese M, González-Varo JP, Mudri-Stojnić S, Riedinger V, Rundlöf M et al., Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecol Lett* **19**:1228–1236 (2016).
- 72 Winfree R, Reilly JR, Bartomeus I, Cariveau DP, Williams NM and Gibbs J, Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science* **359**:791–793 (2018).
- 73 Gilbert F, Syrphid aphidophagous predators in a food-web context. *Eur J Entomol* **102**:325 (2005).
- 74 Jankowska B, Parasitoids of aphidophagous syrphidae occurring in cabbage aphid (*Brevicoryne brassicae* L.) colonies on cabbage vegetables. *J Plant Prot Res* **44**:209–305 (2004).
- 75 Krawczyk A, Hurej M and Jackowski J, Syrphids and their parasitoids from maize crop. *J Plant Prot Res* **51**:93–97 (2011).
- 76 Mohammadi-Khoramabadi A, Lotfalizadeh H and Gharali B, A study on parasitoids of the hoverflies (dipt.: Syrphidae) and their natural effects on them in organic aphid infested lettuce farms of Yazd Province, Iran. *Entomol Gen* **36**:107–115 (2016).
- 77 Rotheray G, Host searching and oviposition behaviour of some parasitoids of aphidophagous syrphidae. *Ecol Entomol* **6**:79–87 (1981).
- 78 Chaplin-Kramer R, de Valpine P, Mills NJ and Kremen C, Detecting pest control services across spatial and temporal scales. *Agric Ecosyst Environ* **181**:206–212 (2013).