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REVIEW

Diptera as predators in biological control: applications and future perspectives

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Abstract The role of dipteran predators in biological pest control programs is reviewed and discussed. Diptera encompasses a large number of potentially efficient predators for biological pest control, yet only a few species are routinary used. The families Syrphidae and Cecidomyiidae provide some of the most successful examples of biological control, but other families (e.g., Muscidae, Sarcophagidae, Sciomyzidae) also include species with that potential. Most applications of Diptera as predators involve the conservation biological control approach, while the augmentative approach has involved only a few species, almost exclusively of Syrphidae and Cecidomyiidae. In a few cases, classical biological control has been employed. Commercialization of species mainly to be used in the augmentative approach is discussed, also focusing on the critical issues linked to rearing methods. The dual services performed by Diptera (pollination as adults and biological control as larvae) have been studied in detail for Syrphidae only, but would deserve further study in other families, e.g., Sarcophagidae. This is the first review in which the use of predatory Diptera in biological control programs is investigated for all families and in all types of applications. This review recommends a multi-taxon approach in the use of Diptera in biological control since a large number of taxa have considerable potential, although this has not yet been tested in practical applications.

Keywords Predatory Diptera · Cecidomyiidae · Chamaemyiidae · Muscidae · Sarcophagidae · Sciomyzidae · Syrphidae · Augmentative Biological Control · Classical Biological Control · Conservation Biological Control · Pollinators

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Introduction

Diptera are one of the most diverse insect orders, with about 170,000 described species in more than 150 families (Evenhuis and Pape 2023). They display a huge variety of structural and ecological traits and include many species of economic importance (Marshall 2012). Diptera are perhaps the most widespread of all insects: they are richly represented in almost every terrestrial and freshwater habitat and have successfully colonized all continents, including Antarctica (Marshall 2012). Although brachyptery (wings reduced) or aptery (wings absent) are known in some Diptera, the adults are usually winged and active fliers. Predatory feeding habits have evolved several times in this group of insects, in both the larvae and adults, even though the legless condition found in all dipteran larvae prevents them from hunting highly mobile prey and the adult mouthparts were originally adapted for sponging or sucking (Marshall 2012).

Zoophagous larvae preying on sternorrhynchous Hemiptera are present in several phylogenetically unrelated families of Diptera: in Chamaemyiidae this is the sole known feeding habit of the larvae, whereas in Syrphinae and Pipizinae (Syrphidae) it is the predominant condition. In other families, aphidophagous larvae are sporadically present in some genera (e.g., *Aphidoletes* and *Monobremia* in Cecidomyiidae; *Cacoxenus* and *Pseudiastata* in Drosophilidae) (Ashburner 1981; Tokuda et al. 2021). Only a few predatory species have been used as aphid biological control agents, under various methodological approaches: classical biological control with Chamaemyiidae, augmentative biological control with *Aphidoletes aphidimyza* (Rondani) and *Feltiella acarisuga* (Vallot), conservation and, recently, augmentative biological control with Syrphidae (e.g., Boulanger et al. 2019; Pekas et al. 2020; Gaimari 2021). The importance of dipteran predators in biological control has prompted some authors to review specific topics related to biological pest control by Diptera. Boulanger et al. (2019) revised biological control by *A. aphidimyza*, focusing mainly on rearing and efficacy in this species. Gilbert (2005) focused on the trophic interactions between hoverflies and other invertebrates, and Rodríguez-Gasol et al. (2020) revised hoverfly ecosystem services. Predatory Diptera were mentioned as natural enemies of aphids in reviews focused on specific crops, such as apple orchards (Zhou et al. 2014) or cereals (Stell et al. 2022). Some predatory Diptera have also been used for the biological control of non-agricultural pests, such as house flies by *Hydrotaea aenescens* (Wiedemann) (Muscidae) or intermediate snail hosts by Sciomyzidae (as reviewed by Murphy et al. 2012).

The aim of this review is to provide an overview of the use of Diptera as predators in biological pest control, highlighting already consolidated applications [e.g., *A. aphidimyza*, *Sphaerophoria rueppelli* (Wiedemann), *Eupeodes corollae* (Fabricius)] as well as the potential of less-studied groups. We included all families of Diptera with larvae and/or adult predators considered potentially useful in the biological control of pest, not only of crops. All types of biological control (classical, augmentative and conservation) were considered, including ecological services (pollination) other than biological control provided by dipteran predators. The discussion is arranged following dipteran families, starting with those used in aphid and mite biological control (Syrphidae, Cecidomyiidae and Chamaemyiidae), followed by Muscidae, Sciomyzidae and Sarcophagidae.

Syrphidae: from biological control to multiple ecosystem service providers

Hoverflies (Diptera: Syrphidae), also called flower flies, are a widely distributed family comprising about 200 genera and 6,000 described species (Courtney et al. 2017). Adult hoverflies usually feed on nectar and pollen, and their ecology is closely linked to these resources. Hoverfly larvae show an exceptionally wide diversity of dietary regimes including zoophagy, saprophagy, phytophagy, mycophagy and coprophagy (Rotheray and Gilbert 2011). Zoophagy is the ancestral condition of the subfamilies Syrphinae and Pipizinae, which represent almost one third of all Syrphidae (Mengual et al. 2023).

Aphids are the most commonly consumed prey, including most of the economically important species. Several hoverflies are generalists, e.g., *Episyrphus balteatus* (De Geer), which has been recorded as preying on 234 species, while other hoverflies have been reported to prey on more than 50 species (Rojo et al. 2003; Gilbert 2005). A few prey specialists are present. For example, *Fagisyrphus cinctus* (Fallén) has been recorded as attacking mainly one aphid species (Rotheray and Gilbert 2011). The genera *Heringia* Rondani, *Pipiza* Fallén and *Pipizella* Rondani, belonging to Pipizinae, prefer aphids that produce wax or flocculence and live in galls (Rojo and Marcos-Garcia 1997). Some genera, such as *Chrysotoxum* Meigen*, Xanthogramma* Schiner and *Doros* Meigen, prey mainly on root aphids, while others, such as *Epistrophe* Walker, *Melangyna* Verrall, *Meligramma* Frey and *Parasyrphus* Matsumura, are adapted for preying on aphids inhabiting trees or shrubby plants (Rotheray and Gilbert 2011). Although aphids are the most common prey, some syrphids may feed on other insects such as leafhoppers, thrips, mealybugs, psyllids, whiteflies or even lepidopteran and beetle larvae, e.g., *Xanthandrus comtus* (Harris), a predator of larvae of the grape wine moth *Lobesia botrana* (Dennis and Schiffermüller) (Rojo et al. 2003).

Prey searching and oviposition behavior in hoverflies are influenced by habitat, plant and aphid characteristics, aphid colony size, semiochemicals and intraguild competitors (Rotheray and Gilbert 2011). Most aphidophagous hoverflies lay a single egg next to or within the aphid, and a reproductive numerical response has been found under field conditions (Hemptinne et al. 1993). Predatory hoverfly larvae are considered highly voracious, although their potential for biological control differs among species. The number of aphids consumed during larval development has been estimated for some species [e.g., *Ep. balteatus*, *Allograpta obliqua* (Say), *Toxomerus marginatus Ischiodon scutellaris* (Fabricius)], with laboratory tests showing some variation (from 130 to 1,300 aphids) based on temperature, hoverfly and aphid species (Tenhumberg 1995; Hopper et al. 2011).

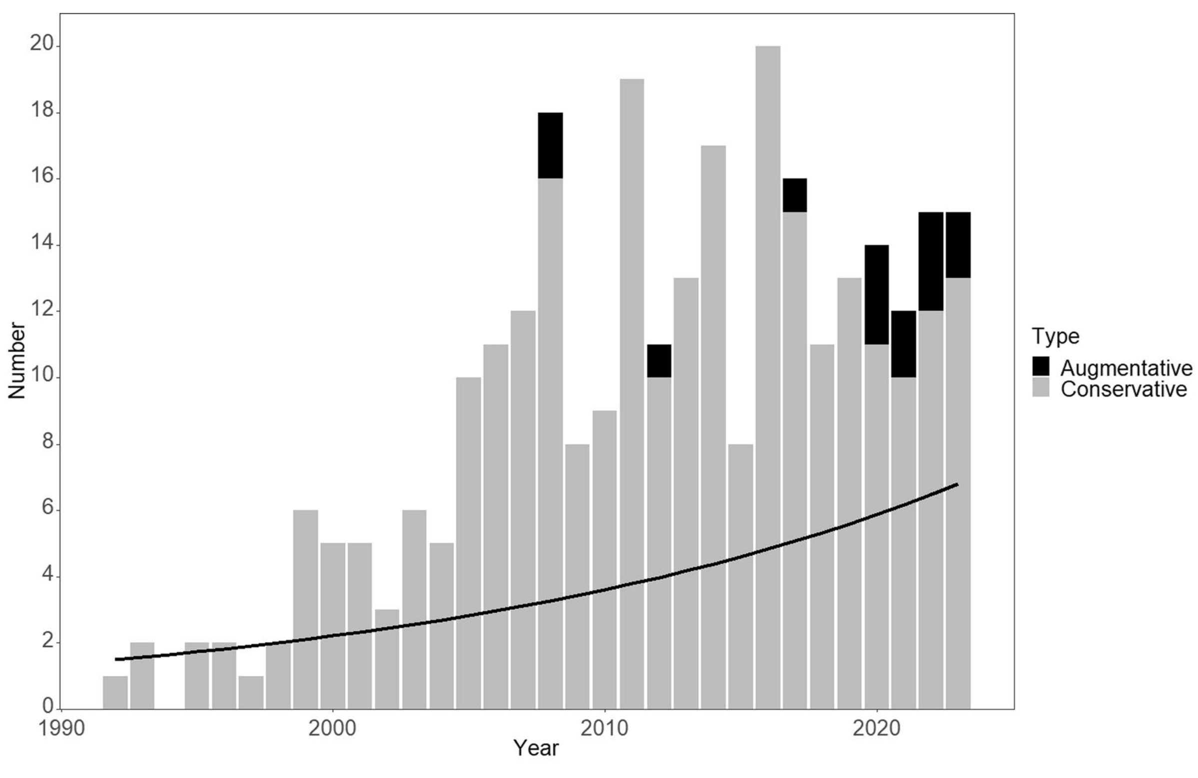

Fig. 1 Number of publications about Syrphidae as biological control agents from 1992 until 2023 (bar), corrected for the general literature growth (black line). Different grey scales are used for publications using conservation and augmentative biological control. No case of classical biological control is present in aphidophagous Syrphidae. The references were obtained using the query “Syrphidae” and “biological control” in Google Scholar and Scopus. Only English language publications in peer reviewed journals were considered. Abstracts from congresses or chapters in books were not included. The black line was calculated starting from 1.5 references in 1991 and adding an annual increase of 5%, as estimated by Bornmann et al. (2021). The complete list of papers is available in Supplementary Table S1.

Predatory hoverflies have long been recognized for their role as natural enemies of aphids and have been used as biological control agents in agricultural landscapes (Chambers 1986; Rodriguez-Gasol et al. 2020). Interest in this topic has significantly increased, albeit with considerable variation from year to year (Fig. 1). The increase in the number of articles detected in Scopus and Google Scholar remains higher than the 5% increase in scientific literature calculated by Bornmann et al. (2021). About 35% of hoverfly species, mostly belonging to Syrphinae, are predators. It has been estimated from faunistic studies that aphidophagous species make up about 60–70% of the total hoverflies recorded in Mediterranean rural landscapes (i.e., northern Italy) (Burgio and Sommaggio 2007; Burgio et al. 2015a).

Hoverflies are among the most abundant aphid predators in many agricultural systems worldwide. In many cases, their role in aphid conservation biological control (CBC) takes place in the context of the so-called "different enemy group", and often the contribution of these dipterans is complementary to that of other predators and parasitoids (Wyss et al. 1999; Gomez Fidelis et al. 2018). It has been demonstrated that *E. balteatus* avoids ovipositing on *Myzus persicae* (Sulzer) colonies parasitized by *Aphidius colemani* Viereck, a potential intraguild prey, confirming that the effect of these two species may be complementary (Pineda et al. 2007). Redundance of food webs can guarantee a seasonal alternation of natural enemies of aphids, ensuring biological control in climatically different seasons or under various conditions (Roubinet et al. 2018). Surplus or redundant antagonist species may become important in an ever-changing environment, as formulated by the hypothesis of spatio-temporal insurance of biodiversity. In such contexts, hoverflies can play a crucial role in many geographic areas and under many environmental conditions.

Crop systems in which CBC by syrphids has been recorded as relevant include cereals (Raymond et al. 2014), sweet pepper (Amaral et al. 2013), lettuce (Gillespie et al. 2011), cabbage (Gomez Fidelis et al. 2018), citrus (Irvin et al. 2021) and soybean (Samaranayake and Costamagna 2018). In some crops and geographical areas, biological control carried out by syrphids can have a decisive role (Bellefeuille et al. 2021; Irvin et al. 2021). For example, in the USA, in crop systems such as organic lettuce, biocontrol of the aphid *Nasonovia ribisnigri* Mosley relies on endemic hoverflies (Smith and Chaney 2007). In Mediterranean greenhouses, particularly in Spain, syrphid species play an important role in biological control in crops such as sweet pepper and eggplant (Pineda and Marcos-García 2008).

In agroecosystems, hoverfly communities are influenced by landscape composition and configuration. However, hoverfly responses can be complex, heterogeneous, season-dependent and species-specific (Burgio and Sommaggio 2007; Meyer et al. 2009; Schirmel et al. 2018). Ecological infrastructures and semi-natural habitats play a crucial role for syrphid reproduction and conservation by providing multiple resources for both adults and larvae, thereby affecting their diversity and abundance (Rojo et al. 2003). In northern Italy, syrphid species richness was found to be positively influenced by herb cover and plant richness, while abundance was dependent on shrubs and length of hedgerows (Burgio et al. 2015b). Landscape parameters strongly influence the abundance of *E. balteatus*: while forest edges provide important overwintering sites, floral environments and herbaceous field margins are the key habitat for this hoverfly during spring (Sarthou et al. 2005). In south-western France, pre-imaginal *E. balteatus* were observed to overwinter within cultivated fields, providing significant biological control of aphids in autumn (Raymond et al. 2014). Several studies have found a positive relationship between the abundance of aphidophagous hoverflies and the proportion of arable crops, probably because these often contain a rich community of aphidophagous syrphid species (Rodriguez-Gasol et al. 2020; Madureira et al. 2023). A negative effect of urban habitat on Syrphidae populations has also been observed, possibly due to habitat fragmentation and reduced resource availability for both larvae and adults (Madureira et al. 2023).

Several factors can seriously reduce hoverfly populations. In northern Italy, the impact of hoverfly parasitoids (mainly Pteromalidae wasps) was higher in simplified landscapes (i.e., monocultures) than in more complex ecosystems, reaching parasitization rates higher than 90% (Sommaggio et al. 2014). Pesticide use in rural landscapes can adversely affect hoverflies, but specific studies on the selectivity of insecticides on hoverflies, including the effects of chronic exposure, are scarcer than for other taxa (Moens et al. 2011; Martins et al. 2024). Hoverflies can feed on honeydew in insecticide-treated crops. Honeydew containing thiamethoxam and imidacloprid was found to be highly and moderately toxic, respectively, to *S. rueppellii* (Wiedemann) (Calvo-Agudo et al. 2019). Because of their importance in biological control and pollination, more attention should be paid to hoverflies as part of standard assessments of the harmful effects of pesticides.

Aphidophagous hoverflies were among the first beneficial targets to be studied in habitat manipulation strategies aimed at enhancing entomophagous performances (Hickman and Wratten 1996). Aphidophagous hoverflies have not been used in any classical biological control program, but in the last decades the number of applications in CBC and, more recently, in augmentative biological control (ABC) has greatly increased (Fig. 1). Several studies and field trials have been conducted using insectary plants to implement CBC, since adults need pollen and nectar to survive and oviposit (Rodriguez-Gasol et al. 2020). The plants providing the best results for hoverflies were phacelia (*Phacelia thanacetifolia* Benth), sweet alyssum (*Alyssum maritimum* [L.]), buckwheat (*Fagopyrum esculentum* Moench) and coriander (*Coriandrum sativum* L.) (Gillespie et al. 2011; Laubertie et al. 2012; Irvin et al. 2021).

Although most uses of hoverflies concern CBC, some aphidophagous species have been successfully employed in ABC, a strategy which entails the mass production of natural enemies. Hoverfly rearing must take into account the nutritional needs of both the adults and preimaginal stages, as well as the mating behaviors of the various species. A large size of the adult cage, along with the presence of a feeding platform, are considered essential features, because most hoverflies mate in flight and rarely visit the cage floor (Frazer 1972). Chambers (1986) observed only 45% successful hatchings for *E. corollae* (Fabricius) and associated low egg viability with infertility, possibly as a result of poor mating. In laboratory conditions, some taxa, e.g., *S. rueppellii*, have been observed to mate while resting, for example on cage walls. Glucose and a mixture of pollen and honey were the food sources that induced maximum longevity in *E. balteatus* (Pinheiro et al. 2015). *Sphaerophoria rueppellii* requires high environmental humidity (> 60%) to complete its development and can develop within a wide temperature range (20–30 °C). It has therefore been considered a good biological control agent of aphids under conditions of high humidity and temperature, such as in Mediterranean greenhouses (Amorós-Jiménez et al. 2012). The use of artificial diets has also been explored for hoverflies. Iwai et al. (2007) successfully reared *E. balteatus* and *Eupeodes bucculatus* (Rondani) larvae on an artificial diet made of drone honeybee brood powder. The addition of fatty acids to the diet was found to improve larval development in these aphidophagous syrphids.

Under conditions such as those in Mediterranean greenhouses, the release methodology of introducing pupae has been reported as little effective: larva and egg releases could lead to more effective biological control, as observed by Wyss et al. (1999) for the augmentative releases of *E. balteatus* against *Dysaphis plantaginea* (Passerini). In this regard, a biological control device consisting of a plastic lamella containing syrphid eggs was set up (Leroy et al. 2010).

Species available in Europe for ABC are *S. rueppellii* and *E. corollae*, currently released in sweet pepper and strawberry greenhouses (e.g., Pekas et al. 2020). A dose of 300 to 600 specimens per hectare is recommended, depending on local conditions. On the American continent, *Eupeodes americanus* (Wiedemann) has been rated as a good candidate for aphid ABC (Outtara et al. 2022) and is commercialized in Canada and the USA (E. Lucas, pers. comm.). This hoverfly species has also been tested against *Acyrthosiphon pisum* (Harris) in commercial greenhouses with banker plants (Bellefeuille et al. 2021), providing an adequate control of the aphid and demonstrating a high application potential.

Due to their dependence on flowers, hoverflies are important pollinators, and their role (as that of several other dipterans) in providing this ecosystem service has recently been reevaluated (Doyle et al. 2020). Using aphidophagous hoverfly species, pest control and pollination have been recorded concurrently, resulting in dual ecosystem services (Pekas et al. 2020; Moerkens et al. 2021; van Oystaeyen et al. 2022). The possibility to increase pollination using hoverflies as biological control agents should be considered when using an augmentative approach on some crops.

For their ubiquitous presence in many terrestrial ecosystems and the exceptional variety of feeding regimes of the larvae, which require a vast range of habitats and microhabitats for reproduction and development, Syrphidae are considered good environmental bioindicators. Bioindication using Syrphidae is facilitated by the taxonomic stability of this family, the relatively easy identification of adult specimens and the availability of an expert system, SyrphTheNet (Speight 2012), enabling the calculation of an ecosystem's conservation state index based on data from this fly family. Examples of the use of Syrphidae as bioindicators were provided by Speight (2012) and Rodríguez-Gasol et al. (2020).

Cecidomyiidae

Gall midges (Cecidomyiidae) are a large family of lower Diptera ("Nematocera"). Nearly 6,300 species of gall midges have been described worldwide, but the true extent of their diversity is still far from fully documented (Hebert et al. 2016; Courtney et al. 2017). Although most Cecidomyiidae are phytophagous, with several species producing galls in plants, the feeding habits of the larvae are highly diverse (Dorchin et al. 2019). A predatory condition probably evolved repeatedly within the subfamily Cecidomyiinae (Dorchin et al. 2019), with larvae preying mainly on aphids or spider mites. Two species of Cecidomyiidae, *A. aphidimyza* and *F. acarisuga*, have been exploited with success in ABC (Boulanger et al. 2019; Tokuda et al. 2021).

Since its first use in Finland at the end of the 1980s, *A. aphidimyza* became one of the most used insects in aphid control (Boulanger et al. 2019). Originally described from Italy, this species has proven to be widely distributed, partly due to introductions (Gagné and Jaschhof 2021; Tokuda et al. 2021). Its larvae prey on a wide range of aphids (almost 80 recorded species; see Tokuda et al. 2021), including *Aphis nerii* Boyer de Fonscolombe and *Aphis asclepiadis* Fitch, which are capable of sequestering chemicals to protect themselves from predators (Boulanger et al. 2019). Predation by *A. aphidimyza* is strongly density-dependent and low aphid infestations can be critical for oviposition (Boulanger et al. 2019). Before feeding on the aphids, the larvae inject them with a toxic saliva that causes paralysis within 1–2 min (Nemec et al. 1992). Usually, the number of aphids killed by the larvae is higher than the number needed to fulfil their nutritional needs, a behavior called "overkill". Before pupation, the larvae drop to the ground and burrow in the soil to a depth of up to 30 mm (Boulanger et al. 2019). Adults of *A. aphidimyza* feed on nectar and/or honeydew, like other gall midges.

Mass production of *A. aphidimyza* has benefited from over 40 years of research, which allowed to improve rearing conditions (see review by Boulanger et al. 2019). Adults mate only once, usually on spider webs (van Lenteren and Schettino 2003). The addition of spider webs in mass rearing cages significantly increases the number of successful matings. As with other entomophagous Diptera, the pupal stage is the one used for storage and shipping in biological control programs, as the pupae do not feed and are more resistant to mechanical manipulation. A questionable aspect is the large interval between release and actual biological control. Even if *A. aphidimyza* adults are less mobile than hoverflies, use of this species seems to be more efficient in greenhouses, especially on sweet pepper and other vegetables (Boulanger et al. 2019). *Aphidoletes aphidimyza* has also been introduced via the banker plant method (or with open rearing units), in some cases together with other beneficials such as parasitoid wasps of the genus *Aphidius* Esenbeck. Good results with this control strategy were obtained for protected cucumber crops (Bennison 1992).

Aphidoletes aphidimyza can be released to reduce aphid populations during rapid growth phases or to prevent the increase of pest density beyond the damage threshold. In the first case, Boulanger et al. (2019) suggested releasing a high number of pupae (1–10 pupae m^{-2}), while in preventive applications the suggested density is 0.1 pupa m^{-2}.

The efficacy of *A. aphidimyza* is greater when its release is combined with that of other aphidophagous insects (Solarska 2004). On the other hand, negative intraguild predation has been observed when other aphidophagous species or predators were present, such as phytoseids, *Orius* Wolff (Hemiptera: Anthocoridae), lacewings, ladybirds and ants (Messelink et al. 2011). Parasitoids can be a serious concern in mass rearings of *A. aphidimyza*, but few data are available on the impact of parasitization under both mass rearing and greenhouse conditions (Boulanger et al. 2019).

Several abiotic factors can seriously reduce the efficacy of *A. aphidimyza* control in crops. RH below

70% can be critical for larval survival, especially if this condition persists for several days (Boulanger et al. 2019). The exposure of eggs and the first two larval instars to high temperatures (35 °C) for a few hours reduces both survival rate and predation efficacy (Wang et al. 2023). A short photoperiod can induce pupal diapause and prevent the appearance of a second generation, while the aphid population may persist. The use of artificial light in greenhouses and/or the genetic selection of strains that do not exhibit diapause seem to be effective in preventing this problem (Boulanger et al. 2019). Chemicals are detrimental for midges, although their effect depends on the type of substance, the number, period and mode of applications and, especially, the midge stage (larvae are more susceptible) (Boulanger et al. 2019). However, available data on the effect of pesticides on beneficial gall midges are still scanty and more research is necessary to better understand the effect of chemicals on *A. aphidimyza* populations under an integrated pest management approach.

In some geographic areas, *A. aphidimyza* specimens occur naturally and play an important role in the CBC of aphids of economic importance, along with other predators. For example, in northern and central Italy, *A. aphidimyza* is recorded as a natural predator of *A. gossypii* in protected cucumber crops (Burgio et al. 1997) and open zucchini crops (Magagnoli et al. 2018). In central Italy, it has been shown that the biological control of *A. gossypii* in organic open field zucchini crops can be achieved in some years through the complex "coccinellids-syrphids-parasitoids". In other seasons, particularly in July, control may be exerted by the dominant *A. aphidimyza* (Magagnoli et al. 2018). This alternance in the predatory guild is probably driven by climatic conditions.

Four species have been described in the genus *Aphidoletes*, all of them with aphidophagous larvae (Gagné and Jaschhof 2021; Tokuda et al. 2021). Among them, *A. urticaria* (Kieffer) has a range of prey and a worldwide distribution similar to *A. aphidimyza*. However, to the best of our knowledge, no application of this species as a biological control agent for aphids has been tested. The potential of *A. urticaria* in biological control should be investigated in order to broaden the range of possible biological control agents belonging to this genus.

The cecid genus *Feltiella* Rübsaamen includes 11 species, all of which predators on spider mites (Gagné and Jaschhof 2021; Tokuda et al. 2021). *Feltiella acarisuga* is the only species of the genus with a worldwide distribution and the only one used, since 1990, as a biological control agent. It has been recorded as preying on several spider mite species, mostly in the genus *Tetranychus* Dufour (Tokuda et al. 2021), but also on Eriophyidae (Gagné and Jaschhof 2021). The larvae of *F. acarisuga* prey mostly on mite eggs and each larva consumes 170–250 eggs to reach pupation (Tokuda et al. 2021). Adult *Tetranychus* mites have also been recorded as prey, but the number of specimens killed per larva was below 50 (Tokuda et al. 2021). The pupae of *F. acarisuga* complete their development on the underside of leaves. Development time from egg to adult depends on the mite species, host plant, temperature and, especially, humidity. A temperature range of 20–27 °C and a RH around 80% (but not lower than 70%) are considered optimal conditions for rearing *F. acarisuga* (Gillespie et al. 2000; Choi et al. 2021). Female fecundity is variable, with 17 to 32 eggs laid per female (Mo and Liu 2006, 2007).

Feltiella acarisuga has been successfully tested in greenhouses to control mites on tomato, pepper, cucumber, strawberry and ornamental crops (Gillespie and Quiring 1997). To maintain an effective population, multiple releases are necessary, usually at a rate of 1,000 per hectare per week. Since in the absence of spider mites the adults move to other sites, Xiao et al. (2011) suggested using infested corn as banker plants. Griffiths (1999) reported an improved control of spider mites when *F. acarisuga* was released together with *Phytoseiulus persimilis* Athias-Henriot. Studies are lacking on the impact of intraguild predation and parasitoids on *F. acarisuga* (Tokuda et al. 2021).

Dicrodiplosis Kieffer is a genus of Cecidomyiidae comprising 12 species, all of them predators of scale insects (Gagné and Jaschhof 2021). Cocco et al. (2021) reported that species of this genus can feed on eggs and crawlers of *Planococcus ficus* Signoret in vineyards, but the efficacy of this predator seems to be low compared to other biological control agents [e.g., *Anagyrus vladimiri* Triapitsyn, *Cryptolaemus montrouzieri* (Mulsant)].

Chamaemyiidae

A small family with 350 known species, also called silver flies (Courtney et al. 2017). The larvae of all species are zoophagous on sternorrhynchous Hemiptera, in particular Aphididae, Adelgidae and Coccoidea. Usually, there is a diet specialization towards both prey and plant. For example, species of *Neoleucopis* Malloch have been recorded only on adelgids (rarely on Margarodidae) on gymnosperms, whereas species of the genera *Chamaemyia* Meigen and *Parochthiphila* Czerny develop on mealybugs feeding on grasses (Gaimari 2021). Larvae of the genus *Leucopis* Meigen develop on a larger range of prey and plants. For example, *Leucopis glyphinivora* Tanasijtshuk has been recorded on more than 75 aphid species (Barriault et al. 2019). Several species have been released worldwide as pest control agents, mainly of aphids and adelgids. The release of *Neulecopis tapiae* (Blanchard) seems to have been effective in controlling *Pineus* Shimer adelgids in Hawaii and New Zealand (Gaimari 1991, 2021). *Leucopis ninae* Tanasijtshuk has been released in North America and Africa. *Neulecopis atratula* (Ratzeburg), *Lipoleucopis praecox* de Meijere and *Leucopis atrifacies* Aldrich have been introduced to Australia, though only *N. atratula* seems to have become established there (Tanasijtshuk 1996; Gaimari 2021). Rarely, silver flies have been released for scale insect control. In the 1960s, *Melaleucopis simmondsi* Sabrosky was released in Brazil against *Insignorthezia insignis* (Browne) (Coccoidea: Orthezidae) (Gaimari 2021). More recently, *Leucopis argenticollis* Zetterstedt and *L. piniperda* (Malloch) were tested against *Adelges tsugae* Annand, which infests western hemlocks in North America (Neidermeier et al. 2020). Mass rearing of Chamaemyiidae has been studied, e.g., by Canale et al. (2002).

Muscidae

More than 5,200 species have been described in this family, including the well-known house fly (*Musca domestica* L.) (Courtney et al. 2017). The family is characterized by an enormous variation in both larval and adult morphology and biology, and a number of species are predators of insects as larvae and/or adults (Marshall 2012).

The genus *Coenosia* Meigen includes 352 described species (Sorokina 2014) known as predators, both as larvae and adults (Kühne 2000). *Coenosia attenuata* Stein is a common species in greenhouses, where the adults prey on several pests such as Aleyrodidae, Sciaridae, Agromyzidae and Cicadellidae (Kühne 2000; Tellez et al. 2009; Seabra et al. 2021). Its larvae are predators in soil, usually on other insect larvae. The species is native to the Mediterranean but is now widely distributed in greenhouses (Kaldor et al. 2022). *Coenosia attenuata* has been suggested as an important control agent of various greenhouse pests (Kühne 2000), and, for this reason, several researchers have attempted to develop an effective method for its mass rearing. Kühne et al. (1994) suggested rearing *C. attenuata* using black fungus gnats of the genus *Bradysia* Winnertz as natural prey. Martins et al. (2015) used *Bradysia impatiens* (Johannsen) and *Drosophila melanogaster* Meigen adults as prey for *C. attenuata* adults in a mass-rearing project. Valentini (2009) tried to rear *Coenosia* larvae using artificial diets, without success.

The larvae of the black dump fly, *Hydrotaea aenescens*, are facultative predators in substrates rich in organic matter. In the presence of potential prey (in particular the larvae of house flies), *H. aenescens* larvae shift from a saprophagous to a zoophagous diet. A *H. aenescens* larva can consume up to 20 house fly larvae per day (Hogsette and Washington 1995). Even if *H. aenescens* is a Nearctic species, its predatory habits were first described from Denmark (Michelsen 1975). This fly has been used to control populations of synanthropic flies, in particular *M. domestica*, in both Europe and North America (Turner et al. 1992; Hogsette and Washington 1995). Unlike *M. domestica*, *H. aenescens* adults prefer shady habitats and rarely leave the ground. For this reason, disturbance to humans or domestic animals is minimal, as is the danger of pathogen transmission. Grønvold et al. (1996) estimated that, in 1994, 5–6% of Danish pig farms used *H. aenescens* as a biological control agent. Hogsette and Jacobs (1999) failed to establish a population of *H. aenescens* in a farm in Florida, USA, probably due to the very wet conditions of poultry manure. Turner et al. (1992) emphasized the importance of chemically treating manure before releasing *H. aenescens*, so as to give it a numerical advantage given its longer developmental time (almost twice as long) compared to *M. domestica*.

Sciomyzidae

Sciomyzidae is a family of acalyptrate Diptera counting 618 species worldwide (Courtney et al. 2017). Apart from three species that prey upon Oligochaeta, Sciomyzidae larvae are all associated with Mollusca, as predators, parasitoids and/or saprophages. The ease of their mass rearing and voracity of the larvae are two key characteristics which have led to the use of Sciomyzidae in the control of harmful snails, through augmentation of natural populations and/or introduction of exotic species. Sciomyzidae have proven to be efficient at containing freshwater snails (Hydrobiidae, Lymnaeidae and Planorbidae) that are intermediate hosts of *Schistosoma* Weinland and *Fasciola* L. flatworms, which are particularly dangerous to humans and livestock (Murphy et al. 2012). In Hawaii, eleven Sciomyzidae species were introduced to control liver flukes, and two of them [*Sepedomerus macropus* (Walker) and *Sepedon aenescens* Wiedemann] became established (Knutson and Vala 2011). However, concerns have been expressed over the introduction of a fly family absent in Hawaii and the possibility that the rich native fauna of terrestrial snails could be attacked (Christensen et al. 2021). In Iran, *Sepedon sphegea* (Fabricius) was mass reared to increment local populations as a measure against snail hosts of *Schistosoma*. Chemicals, especially antihelminthics, were successful in managing flatworms in the late twentieth century. However, the interest in using Sciomyzidae as biocontrol agents persists due to concerns about the emergence of resistance in flatworm populations (Fairweather and Boray 1999).

Use of Sciomyzidae has also been suggested to control slugs that are pests in agriculture (Barua et al. 2021). Few Sciomyzidae have been documented as slug-killing, mainly in the genera *Tetanocera* Duméril and *Euthycera* Latreille (Knutson and Vala 2011). Preliminary studies have suggested *Tetanocera elata* (Fabricius) as one of the species with the highest potential to control slugs. This species behaves like a parasitoid in the first and second larval stages, but becomes a predator (on a wider prey range) in the third stage (Hynes et al. 2014; Ahmed et al. 2019). *Tetanocera elata* preys upon a number of pest slugs, such as *Deroceras reticulatum* (O. F. Müller), *D. laeve* (O. F. Müller), *Tandonia budapestensis* (Hazay), *T. sowerbyi* (Tèrussac), *Arion fasciatus* (Nilsson) and *Limacus flavus* (L.) (Hynes et al. 2014). In Irish agroecosystems, *T. elata* was more abundant near hedgerows, thus proving the crucial role of landscape complexity in enhancing predator efficacy (Bistline-East et al. 2020). Despite the good potential of Sciomyzidae as biological control agents of terrestrial slugs in agroecosystems, no evidence of the use of these flies has yet been documented (Barua et al. 2021).

Sarcophagidae

Flesh flies (Sarcophagidae) comprise some 3,000 named species (Courtney et al. 2017). They are ovoviviparous and their reproductive rate is low, with a pre-larviposition period of about two or three weeks and a clutch size varying from ten to just below 200 (Ferraz 1992; El-Shazly et al. 1995). However, a female may produce more than one clutch and the total number of larvae produced over a female's lifetime may be up to 500 (El-Shazly et al. 1995). Larvae reach maturity in 3–5 days for saprophagous species (Byrd and Butler 1998) and 4–11 days for predatory species (Coupland and Baker 1994; Kuhlmann 1995).

Several species of the Holarctic genus *Agria* Robineau-Desvoidy are predators (often referred to as parasites or parasitoids) of mature larvae or newly formed pupae of moths (Kuhlmann 1995). An extensive research program on the possible use of the Nearctic species *A. housei* Shewell as a control agent of the eastern spruce budworm *Choristoneura fumiferana* (Clemens) (House 1951; Coppel et al. 1959) was discouraging and difficult to interpret (Bartlett et al. 1978). The Palearctic species *Agria mamillata* (Pandellé) was considered for biological control of the apple ermine moth, *Yponomeuta malinellus* (Zeller), in British Columbia (Kuhlmann 1995), although its introduction was apparently never attempted.

The Nearctic flesh fly *Sarcophaga aldrichi* Parker is often considered one of the most important natural control agents in the later stages of forest tent caterpillar outbreaks (Parry 1995). However, while the first instar larvae appear to be able to penetrate healthy pupae before they are fully sclerotized (Hodson 1939), females of this species usually larviposit in or near host pupae that are weakened or dying from disease or other causes, including parasitization by ichneumon wasps, in which case the larva enters via the puncture made by the wasp (Campbell 1963). The high number of moth pupae killed during the later stages of outbreaks may therefore be in part a secondary effect of wasp population increase. *Sarcophaga aldrichi* is often considered a parasite or parasitoid in the literature, but the larva has no particular association with its target and behaves in all respects like a predator, although outsized by its prey.

Sarcophaga (*Heteronychia*) *villeneuveana* (Enderlein) has been used as a biological control agent against a species of Mediterranean conical snail, *Cochlicella acuta* (O. F. Müller), which is a major pest of pastures and grain crops in Australia (Baker et al. 1991). Possible control agents were searched for in the Mediterranean region, which is home to a high diversity of species of the subgenus *Sarcophaga* (*Heteronychia* Brauer & Bergenstamm), likely all of which are predators of terrestrial snails (Whitmore 2011; Whitmore et al. 2013). *Sarcophaga villeneuveana*, *S. uncicurva* Pandellé and *S. balanina* Pandellé were evaluated in quarantine for prey specificity against a range of indigenous Australian snails (Coupland and Baker 1994; Carter and Baker 1997; Baker 2002), and as the latter two attacked several native Australian snails, only the former was released (Baker 2008). *Sarcophaga* (*Heteronychia*) *villeneuveana* was introduced to Yorke Peninsula, South Australia in 2000 (Baker 2002), and an assessment twenty years later found total infestation rates of suitably-sized *C. acuta* to be around 3% (Muirhead and Perry 2021). Although this appears insufficient for effective biocontrol, much higher infestation rates of snails (up to 48%) were observed in sites adjacent to spring- and summer-flowering native vegetation, indicating a potential for local biocontrol in habitats where flies can benefit from the floral resources (Muirhead and Perry 2021).

The western Iberian millipede *Ommatoiulus moreletii* (Lucas) has gained pest status in Australia. A search for possible natural enemies (Baker 1984, 1985) led to the discovery of a species of *Sarcophaga* (*Myorhina* Robineau-Desvoidy) suspected to be a millipede parasitoid/predator (Pape 1990), but this has so far not been studied further.

Other families

Drosophilidae include more than 4,000 known species, and although their larvae are mainly saprophagous, some phytophagous and zoophagous species have been recorded. The genus *Acletoxenus* Frauenfeld, whose larvae are predators of whiteflies, has been suggested as a promising biological control agent in Turkey (Ulusoy and Ülgentürk 2003), China (Yu et al. 2012) and Egypt (Nada et al. 2022). The attempt to introduce *A. indica* Malloch in Cuba as a control agent of the citrus blackfly *Aleurocanthus woglumi* Ashbi failed, probably due to shipment conditions (Clausen and Berry 1932).

The adults of a number of species in several families of Diptera (e.g., Asilidae, Empididae, Dolichopodidae, Calliphoridae) are predators. Asilidae are active predators hunting for flying insects. Their impact on pest insects is not well known and probably limited. On the other hand, they can have a negative impact on plant-pollinator interactions by reducing pollinator numbers and the duration of visits (Benoit and Kalisz 2020). Empididae and Dolichopodidae are small predatory flies dominant in some agroecosystems (Pfister et al. 2017; Bortolotto et al. 2022). They may be important control agents of agricultural pests, e.g., aphids and whiteflies (Cicero et al. 2017; Kheirodin et al. 2019). Recently, the effect of field and landscape management has been studied with the aim of increasing Empididae and Dolichopodidae populations (Pfister et al. 2017; Bortolotto et al. 2022). For example, Kautz and Gardiner (2019) found that agroecosystems can attract long-legged flies (Dolichopodidae). However, landscape simplification and the use of pesticides can strongly reduce the abundance of these predators. Adults of the bengaliine blow fly *Termitoloemus marshalli* Baranov (Calliphoridae) were recently shown to kill thousands of termite soldiers and workers, using the bodies of these insects for oviposition and larval development and potentially leading to the death of the entire colony (Singh and Rognes 2014). The potential for biocontrol of termites by these flies was discussed by Singh and Rognes (2014), but no further studies have been undertaken.

Conclusions

Predatory Diptera are widespread and play an active role as antagonists of insect pests and other dangerous species. However, despite their potential, practical applications of Diptera in biological control have so far been limited to a few taxa. To date, ABC of aphids is a consolidated practice for just a few species, almost exclusively of Syrphidae (e.g., *E. corollae*, *E. americanus* and *S. rueppelli*) and Cecidomyiidae (e.g., *A. aphidimyza*), although additional species have proven to be effective in certain crops and/or geographic areas. For example, rearing of species with different predation strategies, such as those associated with root or gall-forming aphids (e.g., *Pipizella*, *Pipiza* and *Xanthogramma* spp.), would be of interest (Rotheray and Gilbert 2011). More research using a multi-taxon approach would be necessary for CBC strategies aimed at different crops and geographic areas.

Difficulties in mass rearing can be a serious obstacle to the use of more Diptera in ABC. The development of a standardized rearing of *S. rueppelli* and *E. corollae* and the availability of these species on the European market are probably the main reasons for the recent use of hoverflies in ABC projects (e.g., Pekas et al. 2020; Moerkens et al. 2021; van Oystaeyen et al. 2022).

The main challenge associated with the use of dipteran predators in ABC is that the larvae usually serve as the effective control agent, while the adults feed primarily on pollen and nectar. Since pupae have proven, to date, to be the most convenient stage for transportation, there is a significant time gap between release of the pupae and the actual implementation of biological control by the subsequent generation of larvae. It is necessary to further test methods of transport and release also of other stages, i.e., larvae and eggs, in order to reduce this time gap. In addition, since adult dipterans are usually mobile, there is a risk of females ovipositing far from the release point. For this reason, augmentative strategies employing predatory Diptera have proven to be especially effective in greenhouses.

The release of biological control agents using classical approaches may have side effects on non-target organisms, in particular on native natural enemies. For this reason, an Environmental Risk Analysis is required before releasing exotic biological control agents (van Lenteren 2006; Loomans 2021). The release of native predators in augmentative programs is usually considered less dangerous, and therefore regulations are less restrictive (Loomans 2021). However, the sudden increase of one generalist predator following mass release can modify the interaction dynamics among natural enemies. In Diptera, intraguild predation and cannibalism have been extensively studied in hoverflies and, to a lesser extent, in *A. aphidimyza*, usually under laboratory conditions (e.g., Rodríguez-Gasol et al. 2020). Under natural conditions, intraguild predation and cannibalism can be mitigated by habitat complexity, prey availability and low predator density (e.g., Janssen et al. 2007; Ingels and De Clercq 2011). To date, no data are available about the potential alteration of these interactions following a mass release of dipteran generalist predators. For example, mass releases of *S. rueppelli* have increased in recent years and have become a routine plant protection technique in some crops (e.g., sweet pepper, zucchini, strawberries in greenhouses). However, in some geographic areas (e.g., northern Italy), the congeneric *Sphaerophoria scripta* (L.) is the dominant species. It would be interesting to study aphidophagous species dynamics within the predatory guild following a mass release of beneficial dipterans.

Most applications of Diptera as predators involve the CBC approach, highlighting a crucial role of flies in agroecosystems and other habitats with lower degrees of human alteration. In particular, hoverflies are among the first beneficials to be used as predators and bioindicators in the evaluation of habitat management techniques on farms. However, scant information is available about the effects of habitat management on predatory flies, with the exception of hoverflies. Landscape complexity strongly affects biodiversity and ecosystem services in agroecosystems (Martin et al. 2019). Therefore, we need more information on how management at different scales (from field to landscape) can affect dipteran predators used in biological control.

The impact of pesticides on non-target organisms, including beneficial insects, is widely known. However, research on pesticide toxicity on dipteran predators is scanty and usually difficult to evaluate using a comparative approach, since evaluation risk methodologies are not yet standardized. Recently, a standardized methodology of acute contact exposure was developed and applied to three species of Diptera pollinators (Martins et al. 2024). This approach, widely used for bees, is interesting and promising, as it allows for comparative analyses of toxicity data. The first data provided suggest a wide variability in the response of Diptera species to chemicals, but more research is needed.

The role of Diptera as pollinators has usually been underestimated, but an increasing body of evidence highlights their importance also in crop pollination (e.g., Cook et al. 2020a; Doyle et al. 2020). As pollinators, flies and midges differ significantly from bees in several respects (e.g., flower preference and lack of a nesting-centered behavior). Therefore, Diptera are an important component of a diverse and effective pollinator community. However, the mass rearing and release of dipterans for crop pollination is still a little-used practice (Cook et al. 2020a, 2020b). In the case of dipteran predators, a double benefit can be obtained: pollination by the adults and biological control by the larvae. However, the dual services performed by Diptera have been studied in detail only in Syrphidae. This aspect should be further studied in other families, such as Sarcophagidae (Howlett et al. 2016), and should be considered when selecting potential species for release. Both ecosystem services (biological control and pollination) could be obtained through a careful selection of the species to rear and release, using a multi-functional approach.

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Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Research involving human participants and/or animals In the present review, no human participants and/or animals have been involved.

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