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The ecology of predatory hoverflies as ecosystem-service providers in agricultural systems

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ABSTRACT

The main contemporary challenge for agriculture is to meet the food demands of the increasing world population while becoming more environmentally sustainable. One way to achieve this is through the promotion of functional biodiversity and the ecosystem (nature's) services (ES) that it can provide. The Syrphinae subfamily is a widespread group of hoverflies with a high potential for that service. Hence, the present review aims to synthesize the existing literature on this group. This review is divided in three main sections. First, we focus on those aspects of the ecology of hoverflies that are relevant to their role in biological control. These are divided into nutrition, feeding preferences and prey detection of the different developmental stages, overwintering and the effect of landscape on their dispersal and efficacy. Second, we review the ES that predatory hoverflies can provide, particularly pollination and biological control. Finally, we discuss those farming practices that can affect the effectiveness of these Diptera as providers of ES. Overall, this review highlights the potential, as well as limitations and current gaps in knowledge, for enhancing the efficacy of hoverflies as ecosystem-service providers in agricultural systems.

1. Introduction

Increasing use of land, irrigation and agro-chemicals have played a major role in the growth of agricultural production during the “Green Revolution” of the last century. However, it is now recognized that the gains in production were often accompanied by major negative environmental impacts including greenhouse gas emissions, land and water degradation, pollution by agricultural chemicals and biodiversity loss (Tilman et al., 2011; West et al., 2014; FAO, 2017; Pretty et al., 2018). Furthermore, growing human pressure still challenges agriculture as natural resources become increasingly stressed and the demand for food and other agricultural products is expected to increase by 15% in the next 10 years (OECD/FAO, 2019). However, the

dominant priority for agriculture increasingly consists of maximizing food production while substantially shrinking its environmental footprint (Foley et al., 2011; Pretty et al., 2018). A key issue to meet both agronomic and ecological goals is to reduce reliance on external inputs and promote strategies that harness the ecosystem services related to agricultural production (Foley et al., 2011; Garibaldi et al., 2017; Martin et al., 2019) such as pollination and biological control, among others. Hoverflies (Diptera: Syrphidae) are a widely distributed family that comprises three subfamilies, 180 genera and about 6000 described species (Rojo et al., 2003). These insects are life-history omnivores, with the immature stages having different diets than the adults. While the adults usually feed on nectar and pollen from flowers, the larvae have a range of dietary traits, such as saprophagy, phytopy, mycophagy or entomophagy (Gilbert, 1993; Rotheray, 1993).

The Syrphinae subfamily comprises about one third of hoverfly species and can inhabit in a very extensive range of vegetated terrestrial habitats. The group is widespread in all the continents except Antarctica, and is best represented in the Palearctic and Nearctic regions (Irvin et al., 1999; Rotheray and Gilbert, 2011). One of the most significant traits of this subfamily is that the immature stages are predators of aphids (Gilbert, 1993; Rotheray, 1993) and other soft-body insects (see Section 2.1). These predatory hoverflies have long been studied for their potential for aphid biological control in agricultural landscapes (Rojo et al., 2003; Rotheray and Gilbert, 2011), as well as assessing the extent to which they benefit from habitat management practices, such as the implementation of non-crop flowers in otherwise monocultural agriculture (Gurr et al., 2017).

This review has three sections. First, we focus on those aspects of hoverfly ecology that are relevant to biological control and habitat management. These are divided into nutrition (with an emphasis in the nutritional requirements, feeding preferences and prey detection of the different developmental stages), overwintering and the effect of landscape. Second, we review the ecosystem services (ES) that predatory hoverflies can deliver. Finally, we discuss those farming practices which can enhance or reduce the ES (Fig. 1).

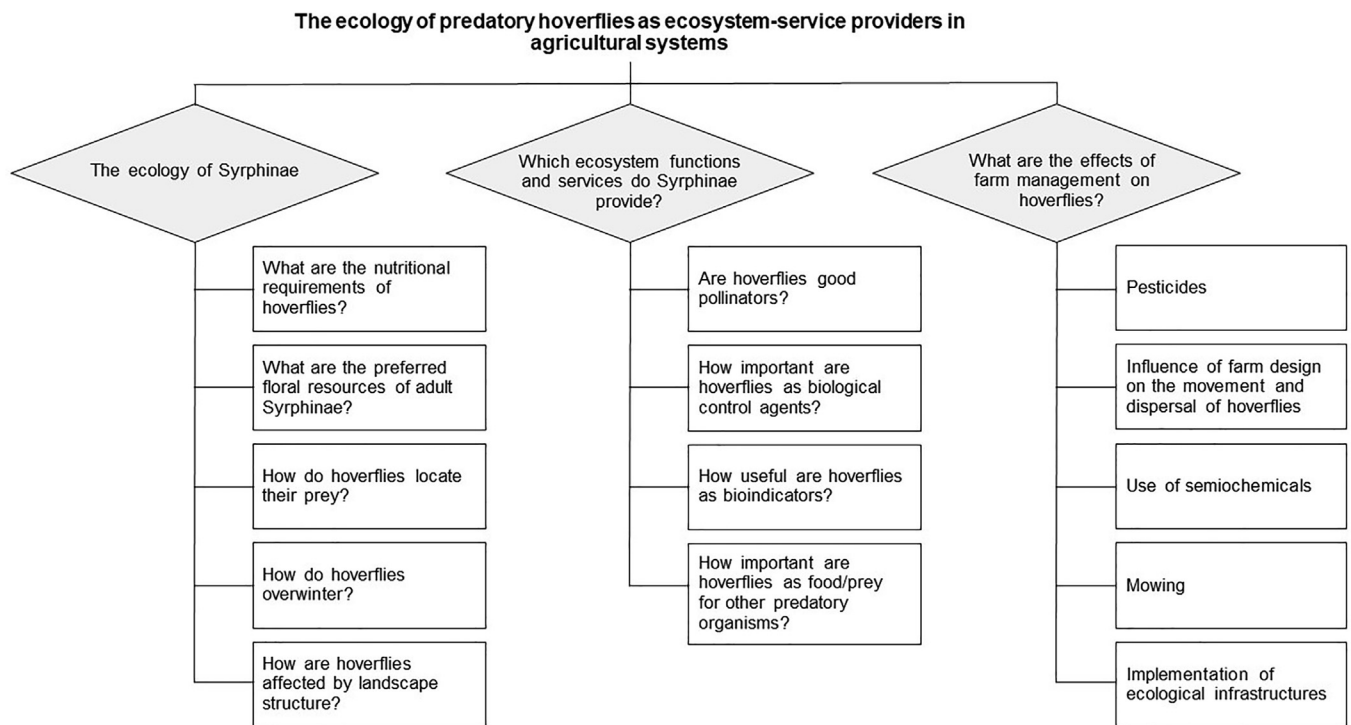


Fig. 1. Schematic overview of the review.

2. The ecology of Syrphinae

2.1. What are the nutritional requirements of hoverflies?

2.1.1. Adults

The ecology of adult Syrphinae is closely related to flowers. Nectar is the main source of carbohydrates. These provide the energy required for survival, while pollen supplies lipids, minerals and the proteins and amino acids that allow sexual maturation and gametogenesis. (Schneider, 1969; Gilbert, 1981; Haslett, 1989a). Most hoverfly species are synovigenic, which means that adults emerge with an immature reproductive system and undergo a pre-maturation period before being capable of mating. During this stage, commonly lasting about a week, both sexes behave similarly. Once mature, however, males need to consume higher sugar amounts to meet the elevated energy demands required for finding females and mating. Females have a higher need for pollen to allow continuous production of eggs (Haslett, 1989a; Gilbert, 1993). This phase can last until death if they do not experience food shortages (Branquart and Hemptinne, 2000a). For instance, females of *Episyrphus balteatus* De Geer, that fed on *Fagopyrum esculentum* (Polygonaceae) Moench flowers only during their preovipositional period, were able to produce eggs for a week thereafter and survive for a further two weeks (van Rijn et al., 2013). Apart from pollen and nectar, aphids' honeydew is also a valuable resource for hoverflies: it can reduce adult foraging time and energy, substituting nectar when flowers are scarce (van Rijn et al., 2006; Pinheiro et al., 2015) and even increase survival when flowers are available (van Rijn et al., 2013).

Diverse food sources (pollen, nectar or honeydew) affect hoverfly fitness and nutritional status in different ways, depending on flower species (van Rijn et al., 2006; Laubertie et al., 2012; Pinheiro et al., 2013a, b, van Rijn et al., 2013; Pinheiro et al., 2015; van Rijn et al., 2016). For example, Laubertie et al. (2012) evaluated the effect of the plants *Calendula officinalis* (Asteraceae) L., *Coriandrum sativum* (Apiaceae) L., *F. esculentum*, *Lobularia maritima* (Brassicaceae) L., *Phacelia tanacetifolia* (Hydrophyllaceae) Benth and *Sinapis arvensis* (Brassicaceae) L. on the fitness of *E. balteatus* and found that individual flower species enhanced different aspects of the fitness of that syrphid: *C. sativum* increased the proportion of fertile females, *F. esculentum* significantly increased longevity and *P. tanacetifolia* increased oviposition rate and lifetime fecundity. Apart from determining the individuals' fitness, adult diet can even affect the survival and performance of the future offspring (Amorós-Jiménez et al., 2014). This points to the potentially important role that a diverse range of floral resources may play in enhancing hoverfly fitness (see Section 2.2).

2.1.2. Larvae

Larvae of Syrphinae are mainly aphidophagous and considered to be highly voracious predators (Rojo et al., 2003). For example, *E. balteatus*, one of the most abundant aphid predators in Europe (Cowgill et al., 1993a; Tenhumberg and Poehling, 1995; Miñarro et al., 2005), is able to consume between 400 and 1000 aphids during its larval development, which lasts about a week under optimal conditions (Tenhumberg, 1995). In general, the predatory efficiency of Syrphinae larvae depends not only on the hoverfly species but also its prey species and its host plant. Syrphinae larvae range from polyphagy to oligophagy. Regardless of their degree of specialization, all such larvae can feed on "peripheral prey" (the larva can feed on sub-optimal prey but suffer declines in its fitness as a consequence) or may be unable to survive on certain aphid species (Sadeghi and Gilbert, 2000a; Short and Bergh, 2004). Moreover, tri-trophic level interactions, in this case, feeding on a single aphid species with different host plants, can also have different effects on larval performance (Vanhaelen et al., 2002).

Although the selection of aphid prey species and aphid-host plant combinations is mainly determined by gravid females (reviewed by Almohamad et al., 2009), hoverfly larvae can also exhibit aphid preferences (Ekukole, 1996; Mizuno et al., 1997; Sadeghi and Gilbert, 2000a; Short and Bergh, 2004; Putra and Yasuda, 2006; Alhmedi et al., 2008), which in some hoverfly species are related to a better performance (Sadeghi and Gilbert, 2000a). With regard to plant choice, larval hoverflies do not exhibit this. Vosteen et al. (2018) found that when larvae have to choose a new aphid colony, they usually select aphids with higher reproductive rates, regardless the type of plant on which the aphids are feeding. Nonetheless, some plant structures, such as trichomes, can hamper the movement of the larvae and therefore their predatory efficiency (Verheggen et al., 2009).

Apart from aphids, hoverfly larvae can feed on other soft-bodied prey such as thrips, psyllids, whiteflies, mealybugs, springtails (Rojo et al., 2003) and lepidopteran larvae (Valentine, 1967; Ashby

and Pottinger, 1974). Some species can even exhibit cannibalism on eggs and first instars of their conspecifics (Belliere and Michaud, 2001). Recently, Vosteen et al. (2018) found that starving larvae are able to feed on non-prey food: individuals that fed on diluted honey and pollen lived about 10 days longer than non-fed individuals, although they could not gain weight or pupate on this feeding regime. Thus, this non-prey food could sustain the larvae at times of poor food supply.

2.2. What are the preferred floral resources of adult Syrphinae?

This group of Syrphinae relies mainly on visual floral cues such the size (Conner and Rush, 1996; Sutherland et al., 1999), shape (Gong and Huang, 2009) and color (Sutherland et al., 1999; Dinkel and Lunau, 2001; Laubertie et al., 2006; Day et al., 2015) of flowers. The latter seems to be crucial for the attraction of hoverflies, as several studies have demonstrated that these insects show a strong preference for yellow (Haslett, 1989b; Sutherland et al., 1999; Laubertie et al., 2006; Lunau, 2014; Rodríguez-Gasol et al., 2019), and that this color can even elicit a proboscis extension response in some species (Lunau and Wacht, 1994; Dinkel and Lunau, 2001). Given that many of these insects feed preferentially on yellow pollen (Lunau, 1995; Lunau and Maier, 1995), this color might be key for locating a food resource. Importantly, this color presented in the field as yellow plastic water traps but with no water enhanced hoverfly oviposition rates on the bean *Vicia faba* (Fabaceae) L. infested with pea aphids *Acyrtosiphon pisum* Harris (Hemiptera: Aphididae) by up to nine times (Day et al., 2015). Nonetheless, other flower traits such as odors (Laubertie et al., 2006; Primante and Dötterl, 2010; Nordström et al., 2017) and quantity of nectar and pollen can also influence hoverflies' decision (Branquart and Hemptinne, 2000b). Hoverflies usually visit the most abundant and rewarding flowers they can find as predicted by simple optimal-foraging theory (Cowgill et al., 1993b; Branquart and Hemptinne, 2000b). In fact, numerous studies have assessed adult hoverfly preferences for flower species and flower mixtures that supply suitable plant resources that can enhance populations of hoverflies and other invertebrate fauna and the ecosystem services provided by them (Colley and Luna, 2000; Ambrosino et al., 2006; Pontin et al., 2006; Hogg et al., 2011; Barbir et al., 2015). However, floral preferences can be modulated by different factors such as plant phenology, presence of other flower species, competition with other pollinators and individuals' previous experience (Cowgill et al., 1993b; Colley and Luna, 2000; Wäckers and Van Rijn, 2012), which can lead to a changing extent of specialisation during the season (Lucas et al., 2018). Due to the different nutritional value of the usually diverse range of food sources and the different relative benefits these provide to the adults' fitness, neither flower visitation rates (which is the most common method to measure flower preferences), nor the presence of pollen in the adult's gut necessarily indicate suitability in terms of realized fitness benefits (Irvin et al., 1999; Laubertie et al., 2012; van Rijn et al., 2016).

The above studies about floral preferences do not necessarily refer specifically to the Syrphinae subfamily, as all Syrphidae adults feed almost exclusively on pollen and nectar or honeydew

(Rotheray and Gilbert, 2011). In fact, only one study has assessed differences between the three Syrphidae subfamilies, in this respect. It showed that Eristalinae and Pipizinae were more specialized than Syrphinae in flower preferences (Klecka et al., 2018). Syrphinae are commonly believed to be generalist flower visitors, visiting mainly actinomorphic plants with flat corollae that provide easily accessible pollen and nectar (e.g. Apiaceae, Asteraceae, Ranunculaceae and Rosaceae) (Branquart and Hemptinne, 2000b). The degree of selectiveness on flower foraging by hoverflies certainly depends on several biological characteristics of the hoverfly species and the individual. Polyphagous hoverfly species, for example those in the genus *Eupeodes*, *Platycheirus* and *Sphaerophoria*, are characterized by elongated mouthparts that enable them to have access to the pollen and nectar of flowers with morphologically concealed corollae. These species are usually more common than specialized ones because they can exploit a wider range of food resources over diverse habitats. In contrast, the species with short mouthparts tend to be oligophagous, feeding mainly on flowers with large inflorescences and accessible nectar (Branquart and Hemptinne, 2000b). It should also be noted that small predatory species, such as *Melanostoma* and *Platycheirus*, also feed on wind-pollinated plants such as grasses and plantains (Leereveld et al., 1976; Branquart and Hemptinne, 2000b).

This is also the case for other natural enemy groups, such as parasitoids (Wratten et al., 2003). Within the same species, the degree of selectiveness can vary depending on intrinsic attributes of the individuals such as their sex, age and nutritional status. For example, as mentioned in Section 2.1, females need more pollen while males are more dependent on nectar (Gilbert, 1981; Haslett, 1989a; Gilbert, 1993; Branquart and Hemptinne, 2000a). In this regard also, gravid females ingest higher pollen amounts than non-gravid ones, and both types consume more pollen than males do (Hickman et al., 1995; Irvin et al., 1999). Age is also a factor as some hoverfly species become less selective as they age (Sutherland et al., 1999; Sadeghi and Gilbert, 2000b; Almohamad et al., 2009). The nutritional status of the individual can have a similar effect as age, as hungry individuals are more likely to be attracted by yellow traps than are satiated ones (Hickman et al., 2001).

2.3. How do hoverflies locate their prey?

2.3.1. Adults

Gravid hoverflies usually oviposit close to their prey because neonate larvae possess a limited dispersal ability (Sadeghi and Gilbert, 2000a; Rojo et al., 2003; Almohamad et al., 2009). However, different strategies are used depending on the hoverfly species, so eggs can also be laid in batches and on plants without aphids (Chandler, 1968b, a; Almohamad et al., 2009). Gravid individuals can discriminate between different prey types, as well as select the prey and prey-plant host combinations that provide better offspring fitness. The factors that can influence the searching and oviposition behavior of aphidophagous hoverflies (from individuals' intrinsic characteristics to external factors such as plant and aphid characteristics) are reviewed in Almohamad et al. (2009). These authors also describe the stages in the location and acceptance

of oviposition sites and the senses involved: visual cues are believed to be the main drivers of host location, followed by olfactory ones. With regard to the latter, some herbivore-induced plant volatiles and aphid alarm pheromone components (such as E-(β)-farnesene, glucosinolates, methyl salicylate, *cis*-3-hexen-1-ol and 2-phenylethanol) as well as aphid honeydew have been identified as eliciting orientation towards the host plant and in some cases even stimulate egg laying, (James, 2005; Zhu and Park, 2005; Almohamad et al., 2009; Leroy et al., 2009, 2010; Mallinger et al., 2011; Leroy et al., 2014; Xu et al., 2018a, b). However, little knowledge exists about the distance over which these compounds are detected. As far as is known, only the Mallinger et al. (2011) work showed off that the presence of methyl salicylate lures attract more hoverflies and green lacewings (*Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae)) which reduced the abundance of aphids on soybeans but the effect disappeared at 1.5 m from the lure.

2.3.2. Larvae

Hoverfly larvae have a limited dispersal capacity, so the oviposition choice of the adult female is the main influencer of the fate of the developing larvae (Sadeghi and Gilbert, 2000a; Rojo et al., 2003; Almohamad et al., 2009). However, it is highly likely that predatory larvae experience food shortages during their development and are forced to move and leave the plant in search of prey. Nonetheless, the larvae of *E. balteatus* do not leave a plant until all the aphids on it are consumed, then they disperse in search of other colonies (Vosteen et al., 2018), being able to move more than 1 m (Chandler, 1969). When searching for a new prey colony, larvae are able to use aphid volatiles (which can occur on living or crushed aphids, concentrated aphid ex-tracts, honeydew or an E-(β)-farnesene solution) to locate aphids that are close but not directly reachable (Bargen et al., 1998; Francis et al., 2005; Leroy et al., 2014). Interestingly, *E. balteatus* larvae exhibit different behaviours to the presence of honeydew depending on their instar. First-instars are highly responsive to honeydew and rapidly orientate themselves to zones impregnated with this substance. Also, both first- and second-instar larvae increase their foraging behavior, moving further and more often in order to reach honeydew sources. Conversely, although third-instar larvae are highly mobile, they do not respond to honeydew (Leroy et al., 2014). To date, no previous work has managed to determine the distance at which hoverfly larvae can detect their prey. However, Francis et al. (2005) found that *E. balteatus* larvae were very sensitive to small amounts of volatiles from aphids: these larvae responded positively to odor sources from a colony of c. 500 aphids while other predators, such as the coccinellid *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) did not respond until the aphid population reached at least 2000 individuals (Han and Chen, 2002).

2.4. How do hoverflies overwinter?

To cope with adverse winter conditions, insects can display diverse ecological strategies including migration and diapause. Moreover, within migratory species, partial migration can also

occur, which consists of a proportion of the population staying to overwinter in the breeding grounds and the others travelling large distances in search of the milder climates (Tenhumberg and Poehling, 1995; Rotheray and Gilbert, 2011). Detailed information of the known overwintering strategies, forms and places of the different European Syrphidae species is given in “Syrph the Net: Species accounts of European Syrphidae (Diptera)”, and expert system that analyzes and evaluates hoverfly communities using the taxonomic value of each species, together with their functional traits and their relationship with the habitat (Speight, 2014).

2.4.1. Migration

Compared to other migratory insects, hoverfly migration is poorly studied. It is best understood in Europe though reports of migration by this insect group also exist in other regions of the world (Shannon, 1926; Westmacott and Williams, 1954; Menz et al., 2019). In Europe, some common species of Syrphinae, such as *E. balteatus* and *Eupeodes corollae* Fabricius, are highly migratory (Wotton et al., 2019). These species migrate annually during autumn travelling large distances to the milder climates of southern Europe, including Mediterranean areas (Tenhumberg and Poehling, 1995; Rotheray and Gilbert, 2011). In spring the offspring of some species of the autumn migrants are thought to make the return northwards. Autumn migration is believed to be achieved in one generation and has been long recognized. Several studies describe overseas migration of hoverfly swarms and others report captures of adult hoverflies over 160 km away from the marking sites in alpine passes in Switzerland (Aubert et al., 1976; Aubert and Goeldlin de Tiefenau, 1981; Rotheray and Gilbert, 2011). Conversely, spring migration has rarely been observed but it is thought to occur over several generations (Raymond et al., 2014b). Recently, a study by Wotton et al. (2019) has demonstrated that mass seasonal migrations of hoverflies (up to 4 billion individuals) occur between the British Isles and mainland Europe, making billions of flower visits and consuming about 6 trillion aphids, therefore possibly providing extensive pollination and biological control services.

Both hoverfly sexes probably migrate with regard to thermal tolerances and metabolic rate but partial migration probably results from the imperatives of their reproductive strategies (Tomlinson and Menz, 2015). However, no physiological studies have investigated the energy requirements for migrating hoverflies (Odermatt et al., 2017). In this regard, *E. balteatus* migrants and overwintering females are less active than summer individuals; that has been attributed to an energy-conserving state in order to overcome adverse conditions (Odermatt et al., 2017).

Genetic studies have demonstrated a lack of genetic differentiation at a continental scale in spite of a great genetic diversity within *E. balteatus* and *Sphaerophoria scripta* L., which suggests a large-scale genetic mixing, probably due to the frequent migratory movements in these species (Raymond et al., 2013b). Moreover, to date neither genetic (Hondelmann et al., 2005; Raymond et al., 2013a; Odermatt et al., 2017), morphological (Raymond et al., 2014b) nor behavioural (Dällenbach et al., 2018) differences occur between migrating and overwintering phenotypes in *E. balteatus*. So it is

possible that individuals share the same genetic material and therefore the capacity for both strategies and that the decision is triggered by environmental or fixed physiological factors (Raymond et al., 2013a; Odermatt et al., 2017). Furthermore, although there is no information available on what triggers migratory behavior in hoverflies, it is possible that migrating flies need to receive the necessary stimuli to continue migrating (Odermatt et al., 2017). Nonetheless, the adult offspring of the migrating phenotypes are more active than those from those overwintering ones. This suggests the involvement of some genetic factors in the migratory tendency, which are expressed only under the appropriate environmental cues (Dällenbach et al., 2018). Further studies are needed to determine the proportion of migratory/resident individuals in a population (Raymond et al., 2013b) as well as the factors that trigger the different overwintering strategies (Odermatt et al., 2017).

2.4.2. Overwintering

Overwintering in hoverflies can occur in the form of larvae, pupae or adults depending on the species. For example, in *Syrphus ribesii* L. overwintering occurs as third-instar diapausing larvae, while in *E. balteatus* the adults are usually the diapausing form (Hart and Bale, 1997). In species in which the adults overwinter, usually mated females in facultative reproductive diapause dominate (Hondelmann and Poehling, 2007). These diapausing females are believed to use only “hiding places” when conditions become harsh and usually remain active during winter (Hondelmann and Poehling, 2007). Winter flight activity has been observed in *E. balteatus* adults at temperatures around 7 °C (Hondelmann and Poehling, 2007). Males, in turn, are thought to be more susceptible to low temperatures, due to their inability to increase their fat bodies (Hondelmann and Poehling, 2007).

Hoverflies do not need special structures to overwinter as they can use a wide range of microhabitats present in the landscape, such as soil, litter, woodlots, caves, tree hollows, cracks, joints between bricks, etc. (Kula, 1982; Hondelmann and Poehling, 2007; Rotheray and Gilbert, 2011). Some aphidophagous hoverfly species have even been reported to be able to overwinter within cereal fields (Raymond et al., 2014a). Nonetheless, in agricultural landscapes, natural and semi-natural habitats will probably favour overwintering hoverflies by providing both undisturbed habitat (Ramsden et al., 2015; Hatt et al., 2017b) and more overwintering sites (Sarhou et al., 2014). In fact, overwintering *E. balteatus* females are positively associated with south-facing forest edges, possibly due to the presence of higher temperatures (Sarhou et al., 2005). In this regard, the model Hover-Winter (Arrignon et al., 2007) gives predictions of survival rate and spatial distribution of an *E. balteatus* adult overwintering population, using landscape and climate data. The model emphasizes not only the importance of shelter availability but also the proximity between feeding and sheltering sites (about 90 m), in order to minimize the energy spent by the overwintering adults and maximize their survival rates. Similarly, the abundance of aphidophagous hoverflies

emerging in the spring is related more to the distance to the nearest semi-natural features than to the amount of land occupied by these features in the surrounding landscape (Raymond et al., 2014a).

Hence, agricultural practices, possibly as a reduction in pesticide use in autumn and a reduction of mechanical weed control in winter, might preserve overwintering populations and therefore enhance biological control in the next season (Raymond et al., 2014a). Moreover, a better understanding of hoverflies' common overwintering places, as well as their activity and nutritional requirements during overwintering, might have important implications in habitat management strategies and early biological control in spring. Furthermore, the largescale connectivity and high dispersal potential evidenced by migratory hoverflies also suggests that management should not be limited to local considerations and that landscape configuration should also be considered (e.g., by ensuring that floral interventions are not confined to one area in the landscape) to maximize hoverfly numbers and efficacy through the ES they provide in agricultural landscapes (Raymond et al., 2013b).

2.5. How are hoverflies affected by landscape structure?

Agricultural intensification commonly implies the maximization of the cropping area at the expense of natural and semi-natural habitats, which frequently become lost or fragmented (Tscharntke et al., 2005). The loss and isolation of these suitable habitats has been acknowledged to negatively affect farmland diversity (Fahrig, 2003; Schweiger et al., 2005; Hendrickx et al., 2007), to the point that nowadays it is considered among the main drivers of the current global biodiversity loss (Tscharntke et al., 2005). Understanding how landscape characteristics affect biodiversity patterns and ecological processes at local and landscape scales is critical for mitigating the negative impacts of agriculture (Tscharntke et al., 2012).

At a landscape scale, its composition (i.e. amount of semi-natural habitat), diversity and configuration (i.e. connectivity) have previously been shown to be key factors in determining plant and animal communities (Fahrig, 2003; Schweiger et al., 2005; Hendrickx et al., 2007). However, evidences on the effects of landscape change on hoverfly populations in agricultural systems is limited, which emphasizes the difficulties of performing these types of studies, as well as the lack of large-scale data (Tscharntke et al., 2012). Nonetheless, general trends are apparent. Hoverfly community structure is associated with the composition of landscape connectivity (Sjodin et al., 2008; Öckinger et al., 2012); but see (Schweiger et al., 2005), the amount of cover of natural and semi-natural habitats or proximity to these (Schweiger et al., 2005; Kleijn and van Langevelde, 2006; Kohler et al., 2008; Sjodin et al., 2008; Meyer et al., 2009; Klein et al., 2012; Öckinger et al., 2012; Medeiros et al., 2018; Jauker et al., 2019); but see (Jauker et al., 2009; Ekroos et al., 2013; Pfister et al., 2017; Hass et al., 2018) and diversity (Sommaggio, 1999; Burgio and Sommaggio, 2007; Meyer et al., 2009; Bommarco et al., 2012; Bourke et al., 2014; Földesi et al., 2016); but see (Schweiger et al., 2005; Ekroos et al., 2013; Hass et al., 2018). Landscape effects on hoverflies can occur at relatively large spatial scales up to 4 km (Haenke et al., 2009; Werling et al., 2011; Power

et al., 2016), but most hoverfly species respond to habitats up to 1 km away (Kleijn and van Langevelde, 2006; Haenke et al., 2009, 2014; Pfister et al., 2017).

The extent to which landscape structure and composition affect the different hoverfly species depends on their ecological traits (Schweiger et al., 2007; Meyer et al., 2009; Moquet et al., 2018). Hoverfly species can be separated into functional guilds according to several life history traits such as larval habitat and feeding behaviour, number of generations per year, adult flight period, body size and dispersal capacity, etc. (Branquart and Hemptinne, 2000b; Ouin et al., 2006; Schweiger et al., 2007; Moquet et al., 2018). Thus, species that belong to specialist guilds might require specific habitats and resources and therefore need to move frequently between habitat patches to acquire specific resources. Highly mobile aphidophagous species such as *E. balteatus*, *E. corollae* and *Syrphus vitripennis* Meigen are usually generalists. These species appear to be less vulnerable to landscape simplification and loss of natural and semi-natural habitats than species in other guilds (Schweiger et al., 2007; Raymond et al., 2014a; Schirmel et al., 2018). Aphidophagous species find prey in aphid colonies from cultivated as well as wild plants (Sadeghi and Gilbert, 2000a; Rojo et al., 2003). They are therefore usually well adapted to agricultural landscapes in this aspect to the point that several authors have even found positive relationships between the abundance and species richness of aphidophagous hoverflies and the proportion of arable crops in the landscape (Burgio and Sommaggio, 2007; Jauker et al., 2009; Meyer et al., 2009; Haenke et al., 2014). Moreover, studies of agricultural intensification are usually performed in landscapes in which natural and semi-natural habitats have already become lost or fragmented to some extent. These hoverfly communities might already be dominated by species which have the abilities to use a wide range of different resources and to reach scattered habitat patches (Tschardt et al., 2012). This might help explain the dominance of aphidophagous syrphid guilds in highly intensified areas (Haenke et al., 2009; Meyer et al., 2009; Haenke et al., 2014; Hass et al., 2018). Nonetheless, previous studies have found aphidophagous hoverflies to be positively influenced by the presence of semi-natural habitats such as forest patches, hedgerows, grass margins, flower strips, grassland, heathlands, etc. (Burgio and Sommaggio, 2007; Kohler et al., 2007; Jauker et al., 2009; Pfister et al., 2017; Medeiros et al., 2018; Schirmel et al., 2018). Woody habitats, such as forests and hedgerows, are usually related to a high availability of larval microhabitats and undisturbed refuges, whereas a higher abundance and richness food resource for adults is usually present in herbaceous habitats. Thus, the different types of semi-natural habitats provide complementarity of resources at the landscape scale (Moquet et al., 2018). Hoverflies require different resources at larval and adult stages, so availability of resources for both developmental stages are necessary (Meyer et al., 2009; Moquet et al., 2018). Hence, food requirements for both stages are not only important for their conservation (Moquet et al., 2018), but also to understand potential responses within a guild to landscape variables. For example, Andersson et al. (2013) found opposing responses to landscape heterogeneity of two highly mobile aphidophagous species: *E. corollae* and *Syrphus torvus* Osten Sacken. While the first primarily preys on aphid species from crops such as beets (*Beta* spp.) which in the study existed mainly in highly

homogeneous landscapes, the latter preferentially preys on aphids from woody habitats, which are more common in heterogeneous landscapes. Therefore, it seems that the abundance of these species is largely determined by the extent and nature of plant diversity on farmland (Andersson et al., 2013).

It is likely therefore that a mixture of natural and semi-natural habitats is necessary to allow the persistence of a diverse range of aphidophagous hoverflies in agricultural landscapes, providing enhanced floral resources for the adults, undisturbed areas in periods of disturbance of the crop (for example during crop harvest or pesticide application) or periods of low resource availability in the crop itself (Bortolotto et al., 2016; Villa et al., 2016). Moreover, the relative importance of diverse semi-natural habitats in providing resources can also change through the seasons (Sarhou et al., 2005; Bortolotto et al., 2016; Villa et al., 2016; Cole et al., 2017). For example, fallow land associated with northern-hemisphere south-facing forest edges can represent an important overwintering site, whereas habitats offering abundant floral resources, such as managed weed strips, become the main habitat for hoverflies in spring (Sarhou et al., 2005). In fact, several studies have recorded more natural enemies and fewer pests in crops close to semi-natural habitats (Stutz and Entling, 2011; Chaplin-Kramer et al., 2013; Alignier et al., 2014; Holland et al., 2016), although this is not always the case (Karp et al., 2018).

Although watercourses do not seem to have a direct effect on those hoverflies that do not have aquatic larvae (Pfister et al., 2017), Ricarte et al. (2011) noticed that in Mediterranean areas, dense colonies of insects, including hoverflies, were observed in shade near bodies of water in woodlands during summer. Therefore, in the case of harsh environmental conditions, these remnant woodlands provide more short-term refuges for hoverflies than do open habitats. Similar activity was recorded in apple orchards during summer, also in Mediterranean areas: hoverflies were often observed flying or resting on the herb layer under tree canopies during the hottest part of the day (Rodríguez-Gasol, personal observation). Hence, the deployment of refuges against high temperatures should also be considered during summer.

It is important to note that landscape structure can strongly interact with local factors, such as farm management practices (Dormann et al., 2007; Haenke et al., 2009; Klein et al., 2012; Andersson et al., 2013; Garratt et al., 2017), modulating their influence on arthropod communities. For example, the attractiveness of flower strips (Garratt et al., 2017) and hedgerows (Haenke et al., 2009) to hoverflies was partly dependent on landscape complexity, with greater numbers of hoverflies seen in areas with a lower local proportions of semi-natural habitat.

3. Which ecosystem functions and services do Syrphinae provide?

3.1. Are hoverflies good pollinators?

Animal pollinators provide a key ecosystem service (being estimated at US\$168 billion worldwide

(Gallai et al., 2009)) by enabling or contributing to the sexual reproduction of the majority of wild and cultivated plant species (Ashman et al., 2004; Klein et al., 2007; Ollerton et al., 2011; Rader et al., 2016). However, the role of hoverflies as pollinators has usually been underestimated, especially in contrast with that of bees (Innouye et al., 2015). Although hoverflies show little specialization at the species level, they exhibit flower constancy as individuals. In other words, they prefer to visit specific flower species by ignoring other potentially attractive species over short time scales (Goulson and Wright, 1998; Fründ et al., 2010; Innouye et al., 2015). Also, hoverflies might contribute differently than bees to pollination services: in fact, it has been demonstrated that the fruit set of several crops increases with non-bee insect visits, independently of bee visitation rates (Klein et al., 2012; Rader et al., 2016). Moreover, hoverflies have distinct biological requirements that might give them a competitive advantage under certain conditions. For example, despite do having one of the most energy-intensive forms of flight (Kevan and Baker, 1983) compared to bees, they have lower energy requirements, being more efficient in harsher habitats and conditions (Ssymank et al., 2008). Also, hoverflies are not central place foragers (animals that return to the same nest in between foraging trips, collecting their food, or food for their offspring, in an area around that nest) since they do not care for their brood, and not forage within a range of a nesting sites as many bee species do. For this reason, they might be able not only to disperse pollen over wider areas, but also to respond differently to landscape structure. In this regard, these non-bee pollinators are not as reliant as are bees on the presence of natural or semi-natural habitat in the surrounding agricultural landscape, which probably makes their pollination services more robust, in relation to changes in land use (Jauker et al., 2009; Klein et al., 2012; Rader et al., 2016).

Few studies have specifically assessed the role of hoverflies (mainly Eristalinae) in the provision of pollination services to wild flowers (Vance et al., 2004; Fontaine et al., 2006) and crops, such as: apple (Solomon and Kendall, 1970; Kendall and Solomon, 1973), strawberries (Kendall et al., 1971; Nye and Anderson, 1974), cranberries (Gervais et al., 2018), sweet pepper (Jarlan et al. 1997), mustard (Mitra and Banerjee, 2007) or oilseed rape (Jauker and Wolters, 2008; Rader et al., 2009, 2011; Jauker et al., 2012). From these, only Jauker and Wolters (2008) and Jauker et al. (2012) have assessed the pollination efficiency of the Syrphinae *E. balteatus*. These authors demonstrated that this aphidophagous hoverfly significantly increased seed set and yield of oilseed rape close to the rate attributable to small honeybee colonies.

A potentially key aspect of hoverfly/flower interactions is the role that pollen minerals play in the fitness of these insects. Pollen mineral stoichiometry does play an important role in honeybee feeding ecology. Certain mineral ratios in pollens from a range of flower species can strongly influence larval growth rates and survival (Filipiak et al., 2017). To what extent this applies to Syrphinae remains to be investigated and could be crucial in selecting floral resources in agroecological habitat manipulation schemes.

3.2. How important are hoverflies as biological control agents?

Biological control can be broadly defined as a reduction of pest populations (pests, pathogens or weeds) by other living organisms, such as predators, parasitoid wasps or microorganisms, providing economic and/or environmental benefit. Worldwide, pest suppression from insect natural enemies, has been valued at over US\$450 billion annually (Costanza et al., 1997). There appear to have been no updates to this figure since this work.

Predatory hoverflies have long been recognized for their potential as natural enemies (Chandler, 1968b; Cowgill et al., 1993a; Gilbert, 1993; Tenhumberg, 1995). Although the potential for biological control differs between species, because of differences in predatory ability (Putra and Yasuda, 2006; Hopper et al., 2011), the larvae are generally considered to be highly voracious. Depending on the larval stage, one larva can consume between 20 and 80 aphids/day, with the third instar preying around the 70% of the total food consumed (Tenhumberg and Poehling, 1995; Samuel and Singh, 2005).

Aphidophagous larvae are usually cryptic and in many cases are inactive during the day; they are mostly active during dawn and dusk (Rotheray, 1993). The adults, in contrast, are day active (Schneider, 1948; Speight, 2014) and possess potentially good ovipositional traits: they are capable of laying eggs continuously during all their life, and they preferentially oviposit in/or close to the aphid colonies (Sadeghi and Gilbert, 2000b). Branquart and Hemptinne (2000a) established that a single female of *E. balteatus* can lay between 2000 and 4500 eggs during its adult life. Moreover, predatory hoverflies are among the most abundant aphid predators in many agricultural systems (Tenhumberg and Poehling, 1995; White et al., 1995; Miñarro et al., 2005; Gardiner et al., 2010; Eckberg et al., 2015) and in contrast to many other aphidophagous insects, they can locate the aphid colonies early in the season (Miñarro et al., 2005; Dib et al., 2010).

These traits make them one of most effective biological control agents of aphids (Dib et al., 2010), with several examples in the literature recognizing their valuable role in biological control (White et al., 1995; Hickman and Wratten, 1996; Schmidt et al., 2004; Hatt et al., 2017a). Despite this, predation by hoverflies is likely to be most effective when it is part of a natural enemy community, with its members having complementary traits (Miñarro et al., 2005; Dib et al., 2010). For example Wyss et al. (1999) found that hoverflies and Coccinellidae together reduced populations of *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae). Similarly, Gontijo et al. (2015) found that colonies of *Eriosoma lanigerum* Hausmann (Hemiptera: Aphididae) were significantly reduced when the hoverfly *Heringia calcarata* Loew was paired with the parasitoid *Aphelinus mali* Haldeman (Hymenoptera: Aphelinidae). However, antagonist interactions can also occur, such as intra-guild predation (see Section 3.4) or cannibalism (Branquart et al., 1997). However, females usually avoid ovipositing in aphid colonies where hoverfly larvae or other predators are already present (Almohamad et al., 2009). Although hoverflies can eat adult parasitoids (Meyhöfer and Klug, 2002) and parasitized aphids, they tend to avoid aphid mummies (Michaud, 1999), either because they are

unable to break open the mummy or because they are unable to recognize these as valuable prey (Meyhöfer and Klug, 2002). Also, ants can strongly interfere with biological control by hoverflies. In this sense, a reduced aphid predation rates have been observed in the presence of ants (Stewart-Jones et al., 2008; Dib et al., 2010).

Another key potential impediment is that because adult hoverflies need to feed on pollen and nectar in order to be able to oviposit, floral resources can be limited in agricultural systems (see Sections 2.1 and 2.2).

3.3. How useful are hoverflies as bioindicators?

Bioindicators are a useful tool in agriculture in helping to evaluate the effects of agricultural practices on the environment. The Syrphidae family is potentially a good taxon for this purpose for several reasons. First, as mentioned above, their larvae present a wide variety of feeding habits. Second, within guilds, many species require different environmental requirements, such as particular macro/ and micro/ habitats for breeding. Third, individuals are easy to find in almost all terrestrial ecosystems, including urban and rural landscapes. Finally, species can be easily identified, at least as adults in Europe (Sommaggio, 1999; Speight et al., 2000; Schweiger et al., 2007). Moreover, given the high mobility of the adults they are probably most suitable for environmental evaluation at large scales (Sommaggio, 1999). In Europe, the role of hoverflies as bioindicators has been assessed in several studies (Sommaggio, 1999; Burgio and Sommaggio, 2007; Billeter et al., 2008; Sommaggio and Burgio, 2014) and particularly acknowledged through the development of the expert system Syrph The Net (Speight et al., 2000).

3.4. How important are hoverflies as food/prey for other predatory organisms?

Adult hoverflies exhibit Batesian mimicry, which consists of a harmless organism resembling a more dangerous one (wasps or bees in the case of hoverflies) to deceive their potential predators (Rotheray and Gilbert, 2011). Many of the larvae, in turn, present a color and patterning that suggests crypsis as a defense against predators (Rotheray, 1981). Hoverflies can still be potential prey of several predators however, such as birds, amphibians, reptiles, spiders and other predatory insects (Rotheray and Gilbert, 2011).

3.4.1. Predatory invertebrates

The most studied aspect of hoverfly predation by predatory arthropods is intraguild predation (IGP), which occurs when the interacting organisms belong to the same guild (i.e. predators competing for the same prey). This type of predation has the potential to affect the biological control outcome. Syrphinae belong to the aphidophagous guild together with mirids, lygids, lacewings, ladybugs,

earwigs and gall midges, among others. Sessile and low-mobility stages of most of these natural enemies are extremely vulnerable to IGP (Lucas et al., 1998). For example, hoverfly eggs are the most susceptible stage and predation rates of 20% and 100% under laboratory conditions can occur (Hindayana et al., 2001; Fréchette et al., 2007). For larvae, susceptibility decreases as they gain in size, strength and mobility. First and second instars are usually more susceptible to predation than are third instars (Hindayana et al., 2001; Fréchette et al., 2007). Nonetheless, the relative body size of the interacting predators also determines the outcome of the confrontation, as usually the larger predator is the one that “wins” (Polis et al., 1989; Lucas et al., 1998). Accordingly, if hoverfly larvae are bigger than the other predator, they are likely to behave as the intraguild predator, showing successful attack behavior. On the other hand, if they are smaller they will be the intraguild prey and display defense and escape behavior mechanisms (Hindayana et al., 2001; Fréchette et al., 2007). Nonetheless, feeding history might also influence these types of behavior, as poorly-nourished hoverfly larvae might be more susceptible to predation due to their lower fitness and ability to defend themselves (Ingels et al., 2015). In addition, feeding specificity can modulate this outcome since more generalist predators have a higher probability of behaving as the intraguild predator, as occurs for example with the extreme generalist *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) (Ingels and De Clercq, 2011; Nedved et al., 2013; Ingels et al., 2015). Furthermore, the abundance of prey can also modify the outcome: the incidence of IGP has been observed to decrease as the availability of more casual prey increases (Janssen et al., 2007; Ingels and De Clercq, 2011); but see (Fréchette et al., 2007). Finally, it is important to note that IGP may be reduced under natural conditions, facilitating species coexistence: a higher habitat complexity implies more refuges, reduced encounter rates and a higher probability of the intraguild prey to escape (Janssen et al., 2007; Ingels and De Clercq, 2011).

3.4.2. Parasitoids

Syrphinae larvae can be parasitized by members of several parasitoid families including the Ichneumonidae, Pteromalidae, Encyrtidae, Figitidae and Megaspilidae (Rotheray, 1993; Rotheray and Gilbert, 2011). Among these, *Diplazon laetatorius* Fabricius (Hymenoptera: Ichneumonidae) is a koinobiont endoparasitoid (parasitoids in which the host continues to feed and to grow after the parasitism event). This hymenopteran parasitizes the eggs or first-instar larvae, with the adult emerging from the syrphid puparium (Rotheray, 1981). This species has been particularly recognized as the most important syrphid parasitoid due to its abundance and frequency worldwide (Rotheray, 1981; Greco, 1997; Jankowska, 2004; Mayadunnage et al., 2009; Mohammadi-Khoramabadi et al., 2016).

To locate their hosts, syrphid parasitoids initially use odors released by the aphid colonies. The parasitoids then use their antennae to locate hoverfly larvae, responding to the contact chemicals present in the larval integument (Rotheray, 1981). When the host is located, females require stimulus from the host haemolymph to elicit egg release, although ovipositor insertions can occur

without egg deposition (Rotheray, 1984). In some other hoverfly parasitoids, movement of the larvae is a necessary final cue to elicit oviposition (Rotheray, 1981). Visual cues seem to be unimportant during this process (Rotheray, 1981). While most parasitoids of Syrphinae are monophagous, a few can be oligophagous (such as *D. laetatorius*) (Rotheray, 1984). Differences in parasitoid host ranges, phenology and target stage of the host (egg, first, second or third instar) probably enable partitioning of resources between possible competitors (Rotheray, 1981; 1984). In the case of a multiparasitized host, the parasitoid emergence depends on the parasitism interval: with a 72-hour pause between multiparasitism, the older parasitoids are usually those that survive. In contrast, if the time interval is lower than 72 h, the latter is going to survive (Rotheray, 1984). The interval between oviposition and adult parasitoid emergence is usually from 10 up to 14 days (Krsteska, 2014).

If parasitized, hoverfly larvae can deploy an immune response to help survive parasitoid attacks. These parasitized larvae can increase their immune response with larval age, so while first instars are not able to survive, a 40% and 100% survival rate was observed in second and third instars, respectively (Hazell et al., 2005). However, this resistance usually implies some life-history costs to the host. For example, larvae of *E. balteatus* attacked by *D. laetatorius* consumed fewer aphids than unattacked individuals and had a lower pupal weight and adult survivorship (Tinkeu and Hance, 1997; Hazell et al., 2005). Hence, parasitoid pressure can decrease larval rate of predation on prey and consequently the top-down effects provided by Syrphinae (Tinkeu and Hance, 1997; Hazell et al., 2005). Despite this, the impact of parasitoids on hoverfly populations has not been widely studied, and in many cases data on parasitization rates are highly variable ranging from almost nil to more than 50% (Krotova, 1993; Jankowska, 2004; Smith and Chaney, 2007; Nourbakhsh et al., 2008; Likhil and Mallapur, 2009; Mayadunnage et al., 2009; Gomez-Polo et al., 2014; Mohammadi-Khoramabadi et al., 2016). Only Sommaggio et al. (2014) assessed the effect of agricultural management on Syrphinae-parasitoid populations. In that study, higher parasitism rates of aphids by hoverfly larvae were found in habitats simplified by intensive agriculture than in more diversified ones.

3.4.3. Birds

Several bird species can feed on hoverflies: chiffchaff (*Phylloscopus collybita* Vieillot (Passeriformes: Phylloscopidae), nuthatch (*Sitta europea* L. (Passeriformes: Sittidae), marsh tit (*Parus palustris* L. (Passeriformes: Paridae), dunnoek (*Prunella modularis* L. (Passeriformes: Prunellidae) (Kristín, 1988) and tree sparrow (*Passer montanus* L. (Passeriformes: Passeridae) (Grass et al., 2017). However, only one study has specifically assessed the impact of birds on hoverfly populations: Grass et al. (2017) found that tree sparrows can feed on aphidophagous insects, to the point that they can even have an impact on aphid populations as hoverfly larvae together with ladybirds can account up to 77% of the sparrows nestlings' diet during times of peak aphid density in arable land systems in Germany.

4. What are the effects of farm management on hoverflies?

4.1. Pesticides

The use of pesticides for pest and disease control can potentially affect non-target organisms. In fact, adverse effects of pesticides on nontarget arthropods have been widely reported and a source of worldwide attention and concern for decades (Moreby et al., 1997; Gil and Garg, 2014). In any attempt to use habitat management to increase the effectiveness of hoverflies as biological control agents, pesticide use can potentially result in major disruptions. However, this is a large topic and the literature is dominated mainly by laboratory studies (Lowery and Isman, 1995; Jansen et al., 1998; Colignon et al., 2003; Jansen et al., 2011; Moens et al., 2011). More complex and realistic attempts to evaluate the effects on hoverflies are rare (Jansen, 2000; Dormann et al., 2007; Qiaoyan et al., 2015).

The International Organization For Biological Control-Western Palearctic Regional Section (IOBC-WPRS) Working Group “Pesticides and Beneficial Organisms” has developed a database on selectivity of pesticides on beneficial arthropods to develop standard methodologies to evaluate the side effects on natural enemies, and to assist organizations and growers to choose selective pesticides in pest management strategies. In the case of hoverflies, 124 active ingredients have been evaluated to date on the Syrphidae family and specifically three species:

E. balteatus, *E. corollae* and *S. vitripennis*. According to the classification by mode of action (MOA) of insecticides and acaricides (Insecticide Resistance Action Committee IRAC), fungicides (Fungicide Resistance Action Committee FRAC) and herbicides (Herbicides Resistance Action Committee HRAC), fungicides usually seem to be harmless to hoverflies, except for two groups (“Chemicals with multi-site activity” and “Sterol biosynthesis in membranes”) which have resulted in being “moderately harmful” or “harmful” in initial toxicity tests and semifield assays. Herbicides have been less frequently tested, despite about 22% of the active ingredients having been found to be harmful to hoverflies in initial toxicity tests. These belong to the group “Inhibition of ALS (branched-chain amino acid synthesis)” and “Lipid synthesis inhibition of ACCase” groups. Insecticides were most harmful. Active ingredients belonging to the “Acetylcholinesterase (ACHE) Inhibitors”, “Inhibitors of Chitin Biosynthesis, Type 0”, “Nicotinic Acetylcholine Receptor (NACHR) Allosteric Modulators-Site I”, “Sodium Channel Modulators” and “Compounds of unknown or uncertain MOA” were among the most harmful. The following groups were the least harmful: “Chordotonal Organ TRPV Channel Modulators”, “Inhibitors of Acetyl COA Carboxylase”, “Inhibitors of Mitochondrial ATP Synthase”, “Mite Growth Inhibitors”, “Mitochondrial Complex I Electron Transport Inhibitors”, “Nicotinic Acetylcholine Receptors (NACHR) Competitive Modulators” and “Ryanodine Receptor Modulators”. Nonetheless, it is important to take into account that the toxicity of the different active ingredients will be modulated depending on the dose, the formulations, the type of test, and the species used for the assays. For detailed information see the “Pesticide Side Effect Database” from the International Organization for Biological and Integrated Control (IOBC, 2019).

At the farm scale, several studies have confirmed the positive effects of ‘non-conventional’ agricultural practices (organic and integrated pest management), not only on hoverfly abundance and richness (Power and Stout, 2011; Andersson et al., 2013; Lu et al., 2015; Dib et al., 2016; Power et al., 2016); but see (Gabriel et al., 2010; Gervais et al., 2018) but also on their visitation frequency to crop flowers (Klein et al., 2012). However, organic farming can permit some pesticides that have potential negative impacts on insects (pyrethrum, neem, etc.), so further studies with more data other than organic versus conventional management practices are needed to pinpoint the real effect of farm management on hoverflies (Gervais et al., 2018). In this regard, it has been demonstrated that heavy pesticide burdens reduce hoverfly communities to robust aphidophagous generalist species (Dormann et al., 2007). It is therefore probable that the high mobility of hoverflies allows the rapid recolonization of pesticide-treated fields, as hypothesized by Gabriel et al. (2010). In fact, as discussed above, interacting effects between farming practices and the surrounding landscape are frequent and important (Klein et al., 2012; Gagic et al., 2014; Power et al., 2016).

4.2. Influence of farm design on the movement and dispersal of hoverflies

Several studies have estimated the ‘spillover’ of insects from floral resources into the crop: the higher estimates of the distances involved are around 250 m for *E. balteatus* (Harwood et al., 1994) to 1 km for *S. pyrastris* (Schneider, 1948). However, how farm design influences their dispersal from the surroundings into crops is poorly known. Breaks in the groundcover vegetation seem to impair hoverfly movement, as they are less likely to cross areas such as dirt tracks, asphalt roads, ploughed fields (Lövei et al., 1998) or creek/hedge combinations (Harwood et al., 1994). Moreover, field boundaries can also restrict their flight, depending on their permeability. Highly permeable structures such as post-and-wire fences do not seem to affect them (Wratten et al., 2003). However, the composition of hedgerows can strongly determine their dispersal, as the more dense the hedgerow, the more restricted is the movement (Wratten et al., 2003). In this regard, despite the fact that benefits of hedgerows and forest patches to hoverflies and other beneficials have been widely acknowledged (Sarhou et al., 2005; Miñarro and Prida, 2013; Haenke et al., 2014; Holland et al., 2016), negative relationships between hoverfly abundance and hedgerow length have been described (Power et al., 2016), as well as with hoverfly dispersal and forest cover in the landscape (Öckinger et al., 2012). This is also generally true for most farmland natural enemies (Karp et al., 2018). Thus, the presence and location of barriers can influence different aspects of hoverflies in the crop, such as recolonization after pesticide-induced mortality (Wratten et al., 2003; Curtis et al., 2019) and spillover from implemented ecological infrastructures.

4.3. Use of semiochemicals

As mentioned above, semiochemicals elicit orientation towards the host plant and can stimulate egg laying. In addition, the combination of intercropping with the use of the semiochemicals (E-

(β)-farnesene and methyl salicylate) has been shown to successfully repel aphids and simultaneously attract natural enemies in wheat-pea intercropping systems (Xu et al., 2018a, b). These authors observed an increase in hoverfly larval abundance and in the rate of aphid parasitism, leading to decreases in aphid populations. Moreover, recent experiments by Wang et al. (2019) have demonstrated that slow release formulations of methyl salicylate can significantly reduce the abundance of *Sitobion avenae* Fabricius (Heteroptera: Aphididae) and attract *E. corollae* in wheat fields. Although more research is needed in this issue, the use of semiochemicals shows promising results.

4.4. Mowing

Although mowing is not considered a harmful practice for natural enemies, it usually implies a reduction in floral resource availability (Noordijk et al., 2009). Therefore, if it is not properly managed it can potentially have negative effects on flower visitors, such as hoverflies, due to temporal limitation of floral resources. To minimize these disadvantages, reducing mowing frequency of the groundcover, field edges and vegetation around ditches, as well as leaving non-mowed areas, are recommended strategies to offer better foraging habitat for natural enemies and pollinators (Horton et al., 2003; Boller et al., 2004; Gervais et al., 2018). For example, Qiaoyan et al. (2015) demonstrated that in alfalfa fields, properly timed mowing was more effective in aphid control than pesticide applications, since the natural enemy populations were maintained. Another study in cranberry crops demonstrated that edge mowing was more important than adjacent semi-natural habitats in the presence of hoverflies (Gervais et al., 2018). On the other hand, the value of semi-natural habitats (e.g. hedgerows, grass strips, managed meadows and roadside verges) can be improved by delaying or moving the cutting dates, to provide enhanced floral resources (Horton et al., 2003; Noordijk et al., 2009; Meyer et al., 2017). Moreover, further positive impacts are possible if mowing strategies are properly implemented to provide a continuous and more diverse flower supply at the local and landscape scales (Meyer et al., 2017).

4.5. Implementation of ecological infrastructures

Habitat management is an important sub-discipline of pest management that aims to promote conservation biological control through the maintenance of favorable habitats and the addition of new ones, such as flower strips and hedgerows (Boller et al., 2004; Gurr et al., 2017). These can enhance natural-enemy populations through the provision of shelter, nectar, alternative prey/hosts and/or pollen (SNAP; Gurr et al., 2017). One approach for managing floral diversity to optimize biological control and pollination involves cultivating the few most suitable flower species for the target insect. In this regard, a considerable amount of research has been done and many flower species have been evaluated in relation to the relative suitability of plant species to adult hoverflies, as well as their effects in the adult's fitness (Colley and Luna, 2000; Ambrosino et al., 2006; Hogg et al., 2011).

However, a multiple-species approach can lead to the delivery of a range of ecosystem services as well as biological control (Laubertie et al., 2012).

Although some insectary plants have been repeatedly tested under laboratory and field conditions, it should be taken into consideration that their relative attractiveness can change depending on the combination of plants tested (Hogg et al., 2011), the hoverfly species involved or the other resources present in the landscape. Furthermore, there is evidence that some native flowers might be as good as the typically evaluated insectary plants which are often not native to the country in which the work is done (Fiedler and Landis, 2007; Isaacs et al., 2009). Thus, floral traits seem to be more important than flower species or diversity *per se* (Pontin et al., 2006; Warzecha et al., 2018; Rodríguez- Gasol et al., 2019). Moreover, in mixed floral vegetation, the number of species of predatory hoverflies is highly correlated with the abundance of only those flowers that have accessible nectar (van Rijn et al., 2016). In addition, it is also important to overlap flowering periods of the plants implemented to allow a continuous supply of pollen and nectar (Colley and Luna, 2000). Regardless of the flower composition, richness and abundance of aphidophagous species are positively correlated with flower density (Haenke et al., 2009) but not to the size of the flower patch (Blaauw and Isaacs, 2014).

A related global synthesis suggests that floral plantings do not enhance yield but do enhance pest control and pollination (Tschumi et al., 2016).

5. Conclusions and future perspectives

This review analyzes the key aspects of the ecology of hoverflies in order to promote their delivery of ES in farmland agroecosystems. Predatory hoverflies have long been recognized for their role as biological control agents due to the voracity of the larvae and the high mobility and continuous egg-laying of the adults. However, only recently and thanks to the emergence of concepts such as ecological intensification, interest in the other ecosystem services such as pollination that they can provide has emerged. Hoverflies have usually been underestimated as pollinators especially if compared to bees; nonetheless, they can provide additional pollination services when bees are restricted by temperature or low availability of natural and semi-natural habitats. Therefore, more studies are needed to evaluate their contribution to crop pollination, especially under landscape intensification scenarios.

Their role as bioindicators in agricultural systems has been mostly studied in Europe with potentially useful good results, though more information is needed about the functional traits and habitat requirements of several species. Although hoverflies usually exhibit mimicry and crypsis, they can still be potential prey to several predators. Current evidence shows that the outcome of interactions with intraguild predators depends on the larval instar, as well as the intraguild predator they are faced to. Nonetheless, these types of interactions are not common under natural conditions and coexistence is most likely to occur. Similarly to others predatory invertebrates, the capacity to resist parasitoid attacks also depends on the larval instar. However, little is known about the impact

of parasitism on hoverfly populations, especially with regard to interactions between parasitism and landscape structure. As for vertebrate predators, there is only one study that reports indirect and negative effects of birds on biological control so, further studies should assess the impact of birds on hoverfly populations.

The presence of flowers with accessible pollen and nectar resources is essential for the maintenance and enhancement of the numbers and fitness of hoverflies. The relative attractiveness of the different flower species relies upon their intrinsic attributes as well as the presence of other flower species. Moreover, different plant species have different effects on the fitness of hoverflies. Therefore, provision of a varied flower supply throughout the year is recommended. Despite a considerable amount of research has been done to identify the most attractive resources to hoverflies, the role of autochthonous species should not be underestimated. These are adapted to the local conditions, as well as can reduce management costs by for example promoting an adequate timing of mowing instead of the implementation of typically insectary plant species. On the other hand, yellow is a strong attractant for hoverflies, probably because it is interpreted as a source of pollen. Nonetheless, further research is needed to identify the common attractive floral traits to better tailor the provision of flower resources. In addition, the location of these flower resources can strongly influence the contribution of hoverflies to biological control. Not only because the presence of barriers can impair adult dispersal, but also because further information is needed about the mechanisms of decision-making by hoverfly females to locate aphid colonies and decision-making during their egg-laying behavior. In this regard, interesting progress has been made with the use of semiochemicals for hoverfly attraction and enhancement of biological control, which can help to avoid the use of detrimental pesticides. Nonetheless, more research is needed to determine the distance at which hoverfly larvae can detect their prey and the minimum volatile concentrations needed to facilitate prey location. Moreover, although hoverfly larvae have been reported to be able to predate non-aphid prey, no studies appear to have assessed their effectiveness as biological control agents of other prey.

As well as the provision of flowers, the presence of refuges also emerges as highly relevant, especially during periods of disturbance of the crop (e.g. pesticide application, tillage) and under harsh environmental conditions or for overwintering. With regard to the latter, further studies are needed to assess: a) Factors that trigger the overwintering and migration strategies, b) What determines the ratio of migratory/resident individuals in a population, c) The energy requirements for migrating hoverflies and overwintering individuals and, d) Common overwintering places.

Important implications for biological control arise from a better knowledge of the mechanisms and requirements for overwintering, such as maintenance of hoverfly populations during winter that results in an early activity in spring. It also is important to emphasize that although aphidophagous hoverflies are usually considered to be less affected by landscape intensification than other hoverfly guilds, the presence of natural and semi-natural habitats as well as increased landscape heterogeneity, are still relevant for the maintenance of hoverfly populations. Landscape structure can strongly

interact with local factors, outweighing practices like application of pesticides and implementation of flower strips, by providing necessary floral resources and undisturbed areas from which hoverflies can recolonize the crops.

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